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The spatial and temporal distribution of Panne macrobenthos in a southern New Jersey salt marsh /

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The Spatial and Temporal Distribution of Panne Macrobenthos in a Southern New Jersey Salt Marsh

by

Alan David Harrison

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Presented to the Graduate Committee
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1989

CERTIFICATE OF APPROVAL

THE SPATIAL AND TEMPORAL DISTRIBUTION
OF PANNE MACROBENTHOS
IN A SOUTHERN NEW JERSEY
SALT MARSH

by

Alan D. Harrison

This thesis is accepted and approved in partial fulfillment of the requirements for the degree of Master of Science.

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To Terry Master for all those rides down the shore, and for never letting me forget I spilled soda in his car on the way.

To my advisor Dr. Sidney S. Herman, for giving me just enough direction to get me through the project, and just enough encouragement, so I didn't quit.

DEDICATION

To my wife Jennifer for the help, encouragement, and love that never let me give up on myself.

TABLE OF CONTENTS

LIST OF TABLES AND FIGURES

Abstract

A study of panne macrobenthos was conducted in the Nummy Island salt marsh in Southern New Jersey during the Summer and Fall of 1987, and the Winter of 1988. Samples of macrobenthos were taken monthly. The pannes were found to have three dominant macrobenthic organisms, a polychaete of the family Capitellidae, a diptern midge of the family Ephydridae, and the Salt Marsh Amphipod, Gammarus palustris. Two types of pannes were described, shallow pannes, ranging from 2 to 10cm deep, and deep pannes, ranging from 15 to 75cm deep. The two types of panne were found to have significantly different densities of amphipods, and midges. The shallow pannes had higher densities of both of these organisms. Polychaete densities were not significantly different. The two panne types were also not significantly different in temperature, salinity or sediment characteristics. The panne macrobenthos were also compared to the that of a nearby tidal creek. Qualitatively none of the three dominant panne species were present in the tidal creeks. The dominant tidal creek species were present in the pannes, but in much lower densities.

INTRODUCTION

Salt marshes are coastal areas that are regularly flooded with tides from the sea. These areas form a gradient between neighboring terrestrial and marine environments, giving them characteristics of both types of environment (Daiber 1982, Teal and Teal 1969). On the mid-atlantic coast of the United States, salt marshes are dominated by cord grass, Spartina alterniflora, and salt hay, S. patens. These two grasses, more than any other species, are responsible for the high level of production in the salt marshes (Daiber 1982, Haines 1977, Nixon and Oviatt 1973, Nixon 1980, Odum 1980, Peterson and Howarth 1987, Siebert and Naiman 1980, Teal 1962, Teal and Teal 1969).

This high level of production serves as the basis for the coastal food chain in many areas (Daiber 1982, Itzkowitz and Guida 1983, Nixon 1980, Odum 1980, Siebert and Naiman 1980, Teal and Teal 1969). Dying Spartina spp. form large amounts of organic detritus which are broken down and subsequently washed into the coastal waters (Daiber 1982, Nixon 1980, Odum 1980). The resulting influx of nutrient rich detritus serves as food for zooplarkton, which in turn serve as food for the many species of fish utilizing the area as spawning and feeding grounds, and as a nursery area (Clymer 1978, Daiber 1982).

Salt marshes also serve as a physical and chemical buffer zone between the ocean and the land. Marshes are good absorbers of wave energy generated by tides or storms, and this keeps coastal land from being washed away. An unprotected shoreline can change drastically in only a few seasons. If a pollution spill occurs along the coast, the marshes tend to hold the pollution, and the Spartina grasses will utilize the nutrients which could otherwise result in eutrophic conditions, large algal blooms, and fish kills.

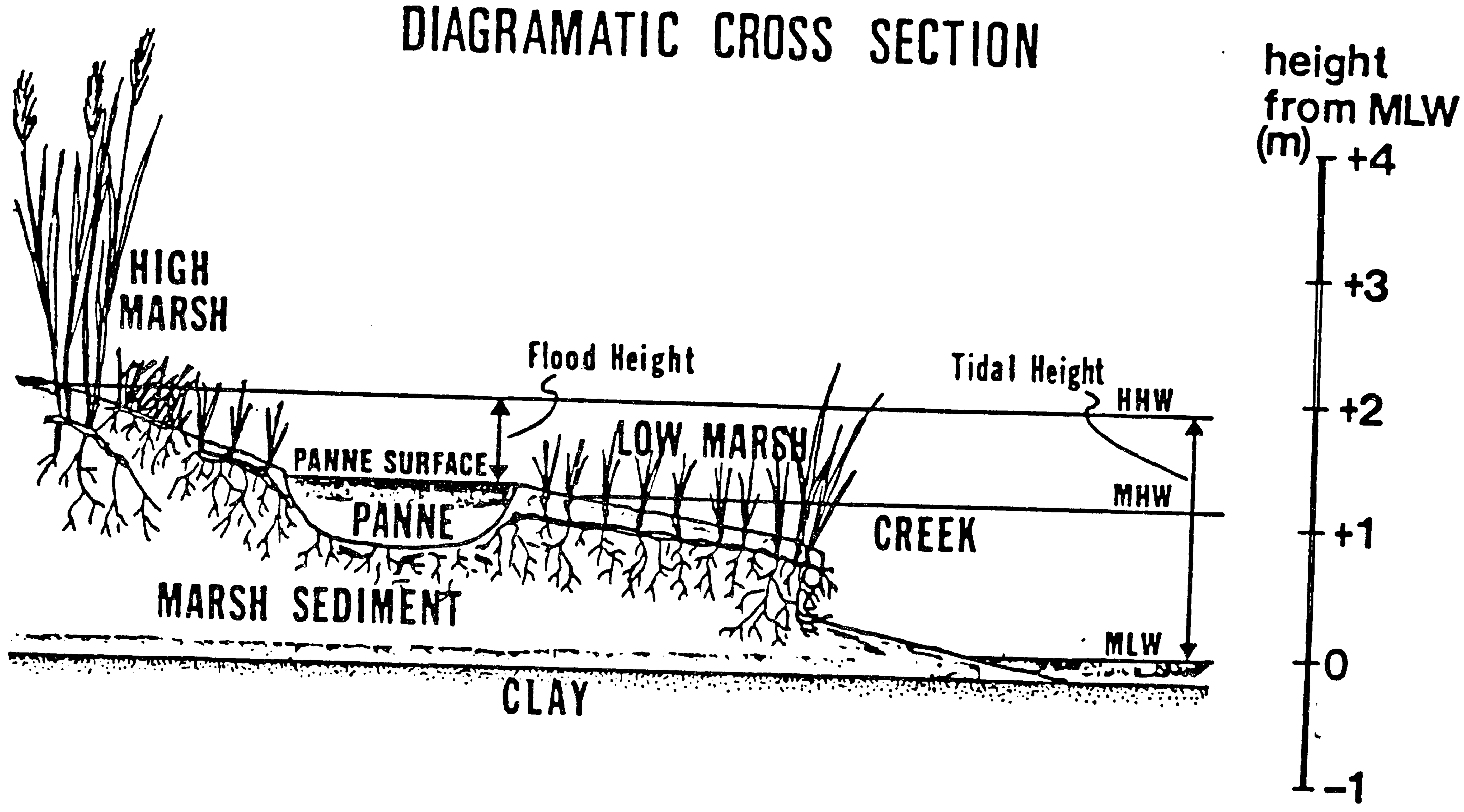
Marshes are also important areas for birds. Many species of birds pass through marshes during their migration, since they are located on a major migratory flyway. The pannes serve as good areas to stop and feed, to store up energy for the migration, and many birds nest and raise their young in the marsh (Diaber 1982, Master 1989).

The focus of this study is on the pannes that are located in great abundance in the South Jersey salt marsh. Pannes are shallow depressions in the marsh, completely surrounded by Spartina, which hold water from the high tides. Figure 1 shows that these pannes are

FIGURE 1

Marsh cross section showing sample panne (Itzkowitz and Guida 1983). Note that pannes only flood during high high water (HHW). This occurs only during the full moon high tides, and occasionally during the new moon high tides.

NJ SALT MARSH:
DIAGRAMATIC CROSS SECTION



unique in several ways. They do not flood on every high tide as do tidal pools, rather they flood only during the highest high tides, around the time of the full moon and occasionally the new moon. This flooding regime keeps the pannes completely isolated, with only a sporadic changing of water except for a few days each month. Because of this isolation, we would expect the pannes to be a harsh environment, with wide flucuations in salinity, temperature, and dissolved oxygen. Master's (1989) work on the same Nummy Island pannes show that oxygen levels do not differ siginificantly between pannes, but they do differ within pannes, over time. In the morning the dissolved oxygen levels are often close to zero and in the evening, oxygen levels approach supersaturation. Some pannes completely disappear between flood tides due to rapid evaporation.

The pannes tend to appear in groups of about 15 to 50 and it is rare to see isolated pannes with no others nearby. It has been estimated that pannes occupy up to 10% of the New Jersey Marsh (Itzkowitz and Guida 1983). Geographically, the pannes exist on the east coast of North America from Nova Scotia to Delaware (Bromley and Bleakney 1979., personal communication; Bruce Coull).

I have been unable to discover any information on the origin of the pannes. It has been suggested in conversation, that their formation may be linked to whether a marsh has an overall influx or outflow of sediment, however, there seems to be no available information on the subject.

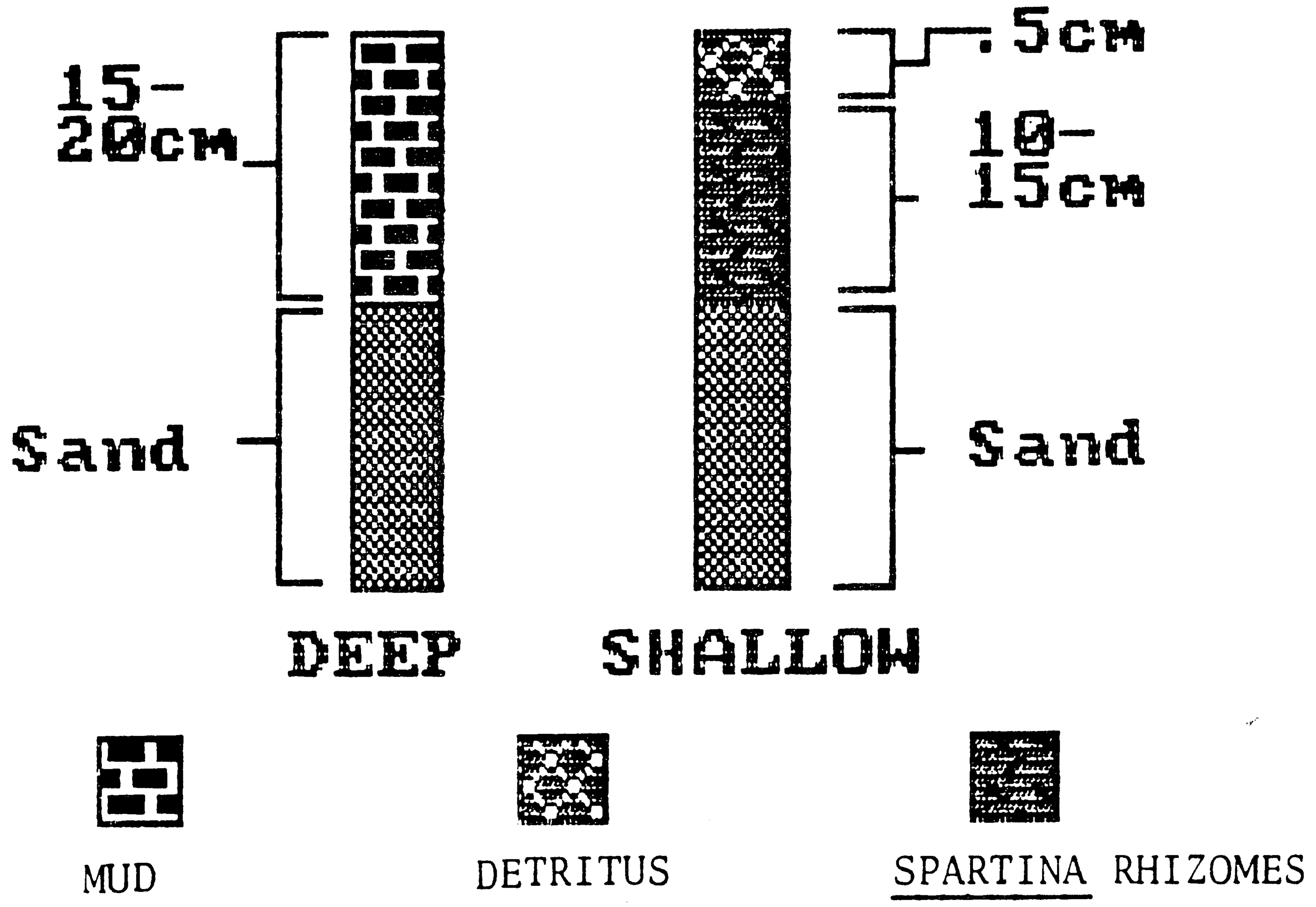
Based on physical differences, two types of pannes may be described: the shallow pannes, ranging from 2 to 10cm deep, and the deep pannes, ranging from 15 to 75cm deep. The shallow pannes all have interlocking Spartina rhizomes in the sediment under the panne, making the sediment very hard. The deep ones have no rhizomes, and they have a very soft mud sediment, which is filled with small fecal pellets (Figure 2). These characteristics may be important, because sediment characteristics are often a driving factor in benthic community dynamics (Sanders 1958, 1960, 1968, and Johnson 1970).

We know that marsh production is important to the food chain of the coastal waters, we also know that the pannes occupy 10% of the NJ salt marsh (Itzkowitz and Guida 1983) so the question arises: What kind of contribution do the pannes make to overall marsh production? According to Clymer (1978), Daiber (1982), and Master (1989), pannes are important sources of food for birds, which feed on the large populations of the mummichog, Fundulus heteroclitis, and the sheepshead minnow, Cyprinodon variegatus, trapped between flood tides (Clymer 1978, Master 1989). The pannes may act as a nutrient processing area because of the large bacterial

FIGURE 2

Panne sediment cross sections showing different layers in each type of panne. Note the 10 to 15cm thick layer of Spartina rhizomes in the shallow pannes.

Panne Sediments - Cross Section



populations which break down Spartina detritus.

The Spartina salt marsh has been well studied on the east coast in both Massachusetts (Bousfield 1973, Nolan 1985, Sanders, 1958, 1960, Short and Short 1984, Wenner and Beatty 1985) and the southern United States, including the Carolinas,(Bell 1980, Bell and Coull 1978, 1980) and Georgia (Odum 1980, Teal 1962, Teal and Teal 1969) However, little information is available on the pannes. In Massachusetts the pannes that exist are different from those in NJ, they flood less often, they have lower salinity levels, they are in marshes dominated by different plants, and very little work has been done on them (Bousfield 1973, Cummings and Ruber 1987, Nolan 1985). In the south there are no pannes in the salt marshes. The most recent work on pannes is that of Bromley and Bleakney (1979) conducted in the marshes of Nova Scotia. However these "pannes" are also dissimilar to those in NJ. The Nova Scotia marshes are dominated completely by Spartina patens, and the pannes flood only during the spring, so that the isolation is in terms of months, and not weeks. There is no detailed work on the concentration or importance of pannes in New Jersey marshes.

In addition to the characteristics described, the New Jersey marshes are traversed by numerous tidal creeks. These are channels of the bay which cut their way into the marsh, without any fresh water source. These creeks meander around the pannes and are often interspaced with the panne groupings. However, they are not connected in any obvious way with the pannes. They differ physically from the pannes, in that they have daily tidal cycles, although they exist in essentially the same areas.

The object of this study is to examine the pannes as distinct from the tidal creeks, and the estuary nearby. The two faunal components in these areas are the plankton, and the benthos. Preliminary study shows that the plankton in the pannes is similar to that in the estuary and the tidal creeks, at least qualitatively (Cummings and Ruber 1987, Personal Communication; Jane Schoeneck). The plankton can also be expected to be washed out with the high tides, every two to four weeks. Preliminary studies show that the benthos living in the pannes is dominated by polychaete worms that live in mucilage tubes, and amphipods that are known to cling to Spartina. Therefore the benthos would be more likely to be long term residents of the pannes. The most obvious difference between the different types of pannes other than the depth, is the sediment. Since the benthic communities are known to vary between sediment types, it was decided that, if there were differences, the benthos would most likely show the greatest variation between the different types of pannes.

Studies of benthos in salt marshes show a rich community that includes many phyla. Daiber's (1982) review of salt marsh fauna includes molluscs, crustaceans, insects, and polychaetes as part of the macrobenthos. In a healthy system, each of these groups can be represented by many different species. In his work from Sapelo Island Georgia, Teal (1962) shows similar results with polychaete densities up to 15/10cm^2 which exemplify typical salt marsh benthic communities. However, none of these studies include any data on pannes. This study is designed as a preliminary investigation into the pannes, and an attempt to show that they are different from the rest of the marsh, at least in terms of the macrobenthos.

Differences in macrobenthic communities are often attributed to differences in sediment characteristics, and the most obvious of these is the difference between sandy, and muddy sediments. Sandy sediments are often dominated by molluscs, and crustaceans, which are absent in muddy sediments, where polychaetes often dominate (Sanders 1958, 1960, Dorges 1977, Rhoads and Young 1970). The reason for these community differences is threefold. Firstly, muddy sediments are fine, and can clog the gills or feeding apparatus of many crustaceans and molluscs, and they afford a poor anchoring place for sessile molluscs (Sanders 1960, Rhoads and Young 1970). Secondly, muddy sediments usually have a higher organic content and deposit feeders, such as polychaetes and molluscs can thrive here (Dorges 1977, Rhoads and Young 1970). Lastly, the polychaetes and molluscs that do live in the muddy areas, are often responsible for a great deal of bioturbation that chokes out forms that are not suited to the finer sediments (Rhoads and Young 1970).

Based on his work on the benthos of Sapelo Island, Georgia, Dorges (1977) divides the marsh into a number of distinct areas. He breaks the intertidal region of the marsh into three sub-areas; the creek banks, which are dominated by the Oyster (*Crassostrea virginica*), the Mud Snail (*Nassarius obsoletus*), and a tube building polychaete, *Diopatra cuprea*. The other two areas, are the streamside levees, dominated by two decopods, the square-backed crab (*Sesarma reticulatum*), and the fiddler crab (*Uca pugnax*), and the barrens, which are inhabited only by *Uca pugnax*. The low marsh is dominated by two bivalves, the ribbed mussel (*Modiolus demissus*), and the oyster (*Crassostrea virginica*), two decapods, *Uca pugnax*, and *Sesarma reticulatum*, and a polycheate, the clamworm (*Nereis succinea*). The current study of the NJ marsh includes the pannes, which do not exist in the Sapelo Island marsh. The pannes exist in areas which correspond to the high marsh, and the barrens in the above study.

In other studies benthic organisms have been divided into the macrofauna, the meiofauna, and the microfauna, and the three are separated according to size (Table 1). Most benthic studies have shown that the most important component of the benthos is the macrofauna. The other two segments of this fauna the microfauna, and the meiofauna are thought to be much less important, at least in terms of production (Bell 1980, Bell and Coull 1978, 1980, Fleeger, et. al. 1982, Gerlach 1971). As a result, it would seem logical, at least in initial studies , to concentrate on the macrobenthos and their environment.

TABLE 1

Size classes of benthic organisms are measured by the smallest sieve size upon which that class can be retained.

SIZE CLASSES OF BENTHIC ORGANISMS

Class	Sieve Size
Macrobenthos	Greater Than .5mm
Meiobenthos	.1 to .5mm
Microbentos	Less Than .1mm

Study Area

The study area was located on Nummy Island, a small island approximately one half mile southwest of Stone Harbor, in Cape May County, New Jersey (Figure 3), at approximately 74 degrees, 47 minutes, 30 seconds West latitude, and 39 degrees, 2 minutes North longitude. This island serves as an ideal area for study because it is completely covered by salt marsh, and the only human traffic on the island is from a road, Ocean Drive, connecting Stone Harbor and North Wildwood, and the occasional bird watcher. The intent was to avoid disturbance, both physical, as with construction, and chemical pollution associated with highly populated areas like Stone Harbor or Atlantic City. There are no buildings on the island, and as far as could be determined, there never have been, so this marsh has never been disturbed, except for the road to be built. The vegetation on this island is dominated entirely by *Spartina alterniflora*.

Figure 4 represents the actual site used for this study, including the panne group used. The individual pannes that were sampled are numbered. The arrangement of the pannes also permitted the opportunity to keep track of any physical changes resulting from tide or

FIGURE 3

Map of Nummy Island and surrounding area (Master 1989). The study site was just east of Ocean Drive, the road running through the center of the Island.

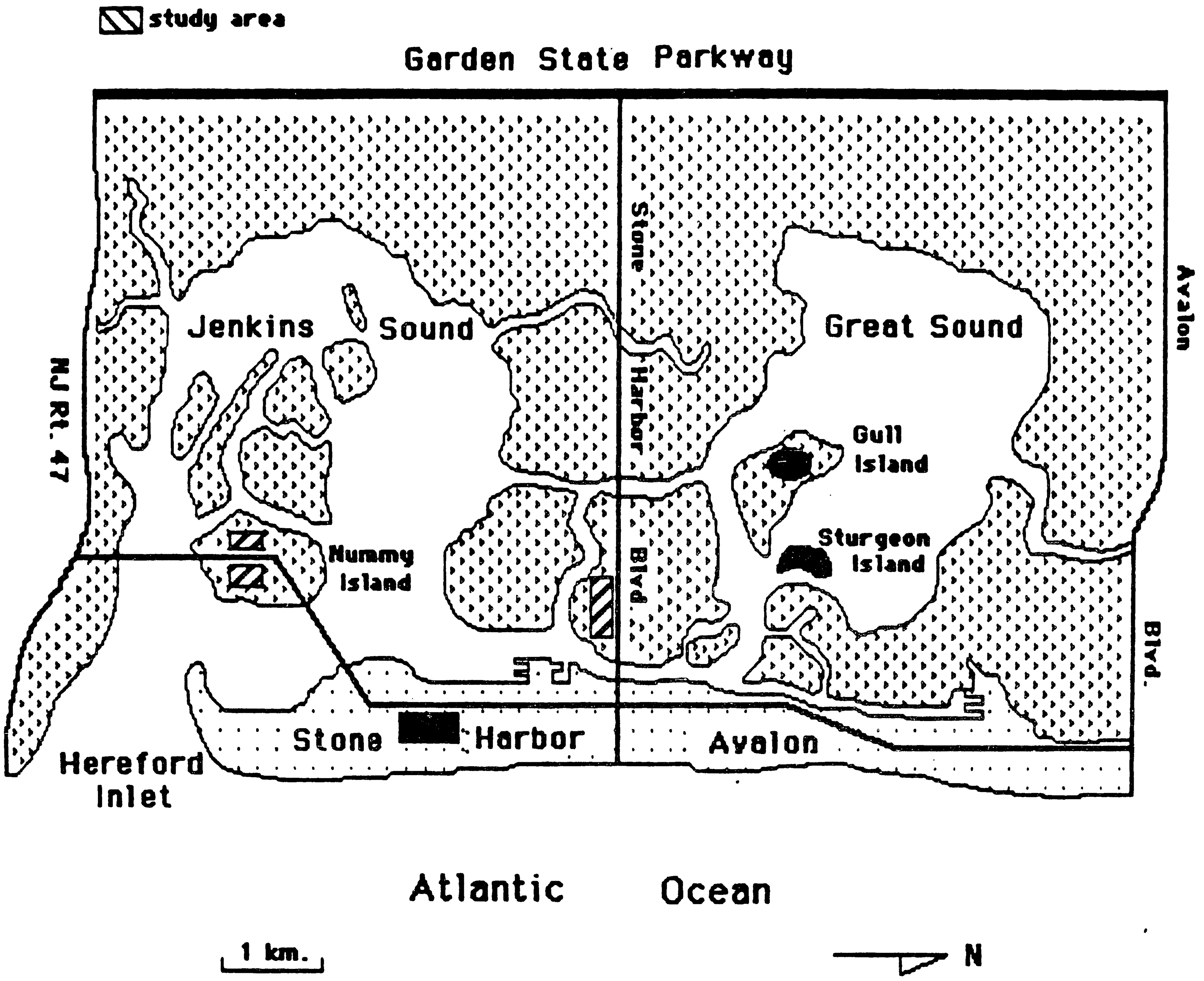
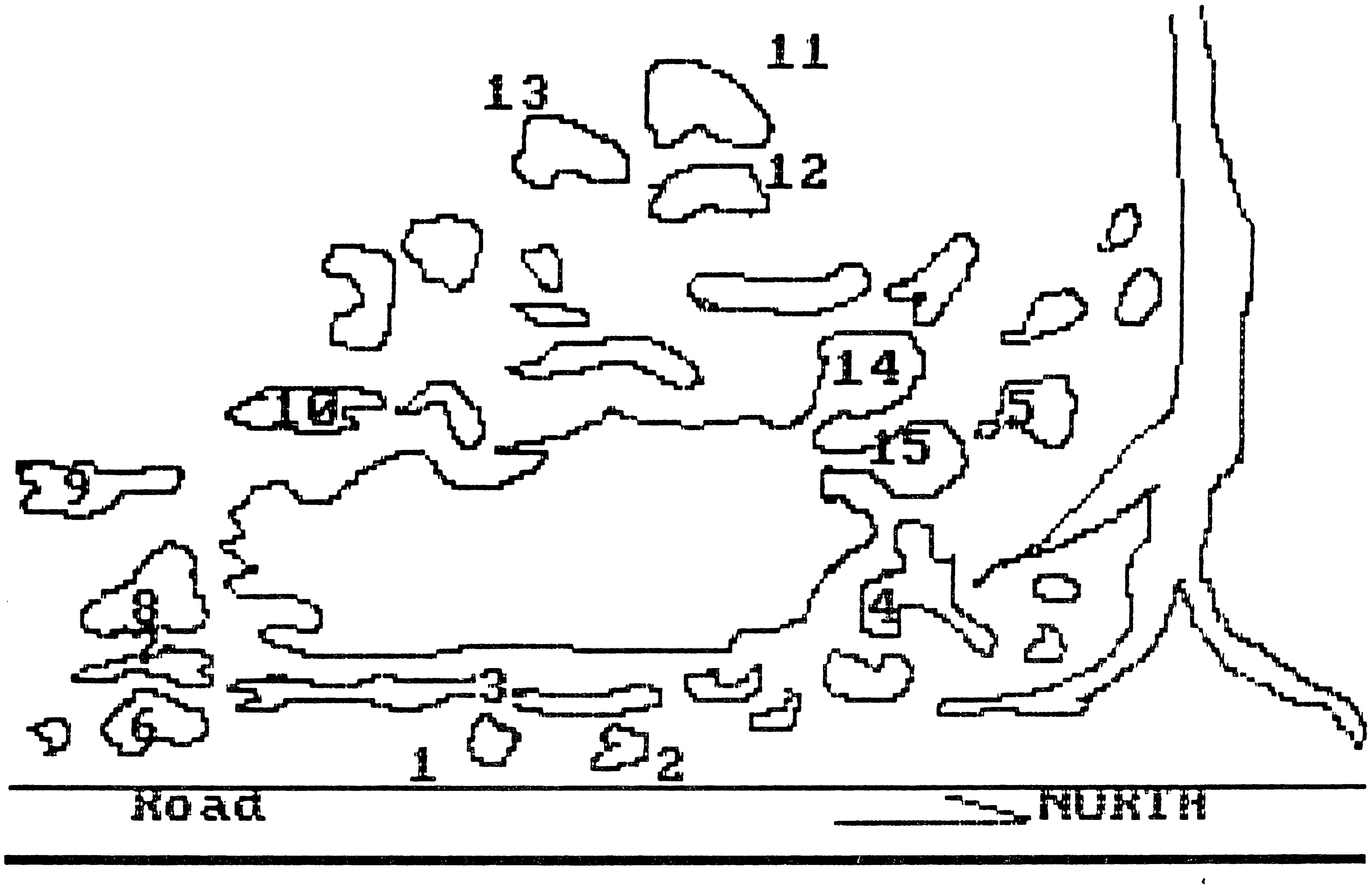

study area
Garden State Parkway
Jenkins
Sound
Great Sound
NJ Rt. 47
Stone
Harbor
Blvd
Avalon
Blvd.
Gull
Island
Sturgeon
Island
Nummy
Island
Stone
Harbor
Avalon
Hereford
Inlet
Atlantic
Ocean
1 km.
N

FIGURE 4

Map of the panne group where the study was conducted. Pannes marked 1 through 15 are the pannes used for sampling. The tidal creek to the right (North) of the panne group was used for the comparative study.


11
13
12
14
10
5
15
9
8
4
7
3
6
1
2
Road
NORTH

storm influences. Pannes marked 1 through 15 were used for the study. Eight pannes, numbers 1, 2, 4, 5, 6, 8, 14, and 15 were shallow, ranging from 2 to 10cm deep, and seven pannes, numbers 3, 7, 9, 10, 11, 12, and 13) were deep, ranging from 15 to 75cm deep.

This study had four main objectives;

1. To develop a description of the panne benthic macrofauna.

2. To compare the two types of pannes, shallow and deep, to see if the physical differences are matched by corresponding community differences.

3. To determine whether or not community differences exist between the two types of panne, and if so, to try to determine factors which may contribute to these differences.

4. To compare the panne benthic macrofauna with that of the tidal creeks.

MATERIALS AND METHODS

Samples of macrobenthos were taken monthly during the period of the study. Along with these samples, temperature, salinity, and depth measurements were also taken at the time of sampling, which was always between 10am and noon. Preliminary qualitative samples were taken in February and March 1987, to help determine if the site was suitable for the study. The study was initiated in June 1987, and samples were collected until October 1987. An additional set of samples was collected in February 1988. Samples were also taken from an adjacent tidal creek for the first three months of the study (Figure 4). Six tidal creek samples were collected the first month, and five were collected each of the next two months, for a total of sixteen. Sampling was done with a two inch diameter core sampler. Further samples were not taken here because of a storm that washed away the tidal creek.

Two core samples with a 2 inch diameter were taken from each of the 15 study pannes monthly. In order to preserve the original environment, and allow space in each panne for samples to be taken each month, core samples were taken sparingly. All the samples were processed by hand under the dissecting microscope.

Standard techniques using geological sieves to separate the fauna could not be utilized because of the high amount of Spartina rhizomes, large detritus, and the delicacy of some of the organisms. The organisms were preserved in 10% borax buffered formalin, and kept for later identification. The following references were used for identification, Fauchald, 1977; Bousfield, 1973; and Gosner, 1979.

Temperature was measured with a standard laboratory mercury thermometer inserted 1cm into the sediment at the time of sampling. Small water samples from each panne were sealed in vials, and taken back to the lab for salinity readings, using the refractometer. These salinity measurements were taken in the field and the lab for the first two months. Since there was no difference in the field and lab results, all further readings were taken in the lab to save time in the field.

An experiment was designed to determine if the absence of amphipods and midges in the deep pannes was due to predation by the two fish species, Fundulus heteroclitus and Cyprinodon variegatus, which were present only in these pannes. This experiment was conducted in five deep pannes, 7, 9, 11, 12, and 13, (See Figure 4), from August 15 to October15, 1987. Ten cylindrical enclosures were constructed, each enclosing .1 $meter^2$. They were made from plastic mesh with openings of 2mm square. Two enclosures were placed in each panne and secured to the bottom with wooden stakes. Into one of each pair was placed a number of fish equalling the average density in the panne (Master 1989), to simulate natural conditions in the panne. The other enclosure in each panne was empty, and was designed to keep the fish out. The null hypothesis, that the differences between pannes is not caused by fish predation would have to be accepted if there were no difference between the benthos in the two enclosures at the end of the experiment. The presence of midges and amphipods in the enclosure without fish at the end of the experiment would indicate that the fish were the cause of their absence in the deep pannes. On October 15, regular macrobenthos samples were taken to see if the exclusion of fish from the empty enclosure had any impact on the macrobenthos.

Silt/Clay fractions were separated using a graded series of sieves (Soil Survey Staff 1951). This measure was chosen because it gives a simple number which expresses the percent of the sediment which is the smaller fraction, silt/clay, as opposed to the larger fraction, gravel/sand. The higher the number, the higher the percentage of the sediment which is small grained, therefore muddy sediment has a high silt/clay fraction, and sandy sediment has a lower silt/clay fraction.

Statistics

All of the samples were treated using non-parametric statistics, because the data were not normally distributed. The statistical tests used, were the Wilcoxon Mann-Whitney U statistic, and Lord's test for two independent samples. (Snedecor and Cochran 1980) Significance was indicated at the 5% level. The Wilcoxon Mann-Whitney U statistic is a test that uses assigned ranks to compare two samples. It is useful when sample sizes are small, and the data are not normally distributed. Lord's test for two independent samples is also a nonparametric test for two samples. I used this test because it is similar to the student's t-test, however, it substitutes the range of the data for the standard deviation as part of the statistic. Simple linear regressions were also used to test for correlation between faunal variation, and temperature, or salinity. These tests were used to determine if there were differences between deep and shallow pannes in terms of the dependent variables (macrofauna populations), and the independent variables (temperature, depth, salinity, and sediment characteristics).

RESULTS

Preliminary Investigation

Preliminary qualitative samples were taken in February and March of 1987. These samples showed only one dominant organism in both types of pannes, the polychaete, (Family; Capitellidae). There were very few midges, and no amphipods in these samples. The samples were taken equally from deep and shallow pannes.

Comparison with Tidal Creeks

The list of organisms collected (Table 2) and their densities (Table 2a) clearly show that there are three dominant organisms in the pannes and two dominant organisms in the tidal creeks. In the pannes the salt marsh amphipod, <u>Gammarus palustris</u>, the dipteran midge of the family Ephydridae, and the unknown polychaete of the family Capitellidae are the three dominant species. I was unable to identify the genus or species of the polychaete collected, and I believe it to be a new genus and species. All of the taxonomic characteristics used to identify the species were present, but they did not match any known species, although it was clearly of the family Capitellidae. The character used to identify down to genus was the number of thoracic segments with only capillary setae. The polychaetes from the panne had nine

TABLE 2

Total number of organisms collected in pannes and tidal creek over the entire course of the study. A total of 180 samples were collected in the pannes, and a total of 16 samples were collected in the tidal creek before it disappeared due to storm induced changes in the marsh.

SPECIES LIST (PANNES)

Species	Number Collected
Phylum: Annelida	
Class Polychaeta	
Capitellidae	113
Unknown (9 Species)	19
Nereis sp.	6
Phylum: Arthropoda	
Subphylum Uniramia	
Superclass Insecta	
Ephydridae	387
Order Diptera	3
Order Coleoptera	3
Order Odonta	1
Subphylum Crustacea	
Gammarus palustris	320
Phylum: Mollusca	
Class Gastropoda	
Nassarius obsoletus	5
Class Pelecypoda (Bivalvia)	
Modiolus demissus	1

SPECIES LIST (TIDAL CREEKS)

Phylum: Mollusca	
Class Gastropoda	
Nassarius obsoletus	33
Class Pelecypoda (Bivalvia)	
Modiolus demissus	4
Mytilus edulis	2
Phylum: Annelida	
Class Polychaeta	
Nereis sp.	14

Table 2a

Overall mean density and standard deviation for organisms found in pannes and tidal creek. High standard deviations for some of the organisms are caused by uneven distribution over time. Some of these organisms had very high densities during one sampling period, and were not present during other sampling periods.

SPECIES LIST (PANNES)

Species	Mean Density #/10cm²	Standard Deviation
Phylum: Annelida		
Class Polychaeta		
Capitellidae	0.3591	0.8418
Unknown (9 Species)	0.0521	0.0486
Nereis sp.	0.0164	0.0052
Phylum: Arthropoda		
Subphylum Uniramia		
Superclass Insecta		
Ephydridae	1.0608	4.1976
Order Diptera	0.0058	0.0019
Order Coleoptera	0.0058	0.0019
Order Odonta	0.0006	0.0006
Subphylum Crustacea		
Gammarus palustris	0.8772	3.2564
Phylum: Mollusca		
Class Gastropoda		
Nassarius obsoletus	0.0137	0.0772
Class Pelecypoda (Bivalvia)		
Modiolus demissus	0.0027	0.0007

SPECIES LIST (TIDAL CREEKS)

Phylum: Mollusca		
Class Gastropoda		
Nassarius obsoletus	1.0176	1.5337
Class Pelecypoda (Bivalvia)		
Modiolus demissus	0.1234	0.0487
Mytilus edulis	0.0617	0.0284
Phylum: Annelida		
Class Polychaeta		
Nereis sp.	0.4317	0.4724

segments of this type. This places it between the genus Leiocapitellides, with eight segments with only capillary setae, and the genus Neoheteromastus, which has 12 segments with only capillary setae. In the tidal creeks, the clamworm, genus Nereis, and the mud snail Nassarius obsoletus, dominate. This table also shows that there is virtually no overlap in species between the pannes and the tidal creeks. The total number of organisms collected were 858 in the pannes in 180 samples, over six months, and 53 in the tidal creeks in 16 samples, over three months.

Comparison of Panne Types

The actual number of organisms collected in the study, broken down by each panne may be seen in Appendix I. When these data are compared individually panne to panne, there is no pattern. It was decided, that to test for faunal and physical differences between shallow and deep pannes, the data for these groups could be summed, and the mean taken for each sampling date as a representative of levels in all of the shallow or deep pannes. These results are shown in figures 5, 6, and 7. The data were then tested using Lord's test for two independent samples, This test showed a difference between the amphipods, (Gammarus palustris), and the midges, (Family; Ephydridae), in the shallow and deep

FIGURE 5

Average amphipod density for each sampling date in shallow and deep pannes.

segments of this type. This places it between the genus *Leiocapitellides*, with eight segments with only capillary setae, and the genus *Neoheteromastus*, which has 12 segments with only capillary setae. In the tidal creeks, the clamworm, genus *Nereis*, and the mud snail *Nassarius obsoletus*, dominate. This table also shows that there is virtually no overlap in species between the pannes and the tidal creeks. The total number of organisms collected were 858 in the pannes in 180 samples, over six months, and 53 in the tidal creeks in 16 samples, over three months.

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FIGURE 5

Average amphipod density for each sampling date in shallow and deep pannes.

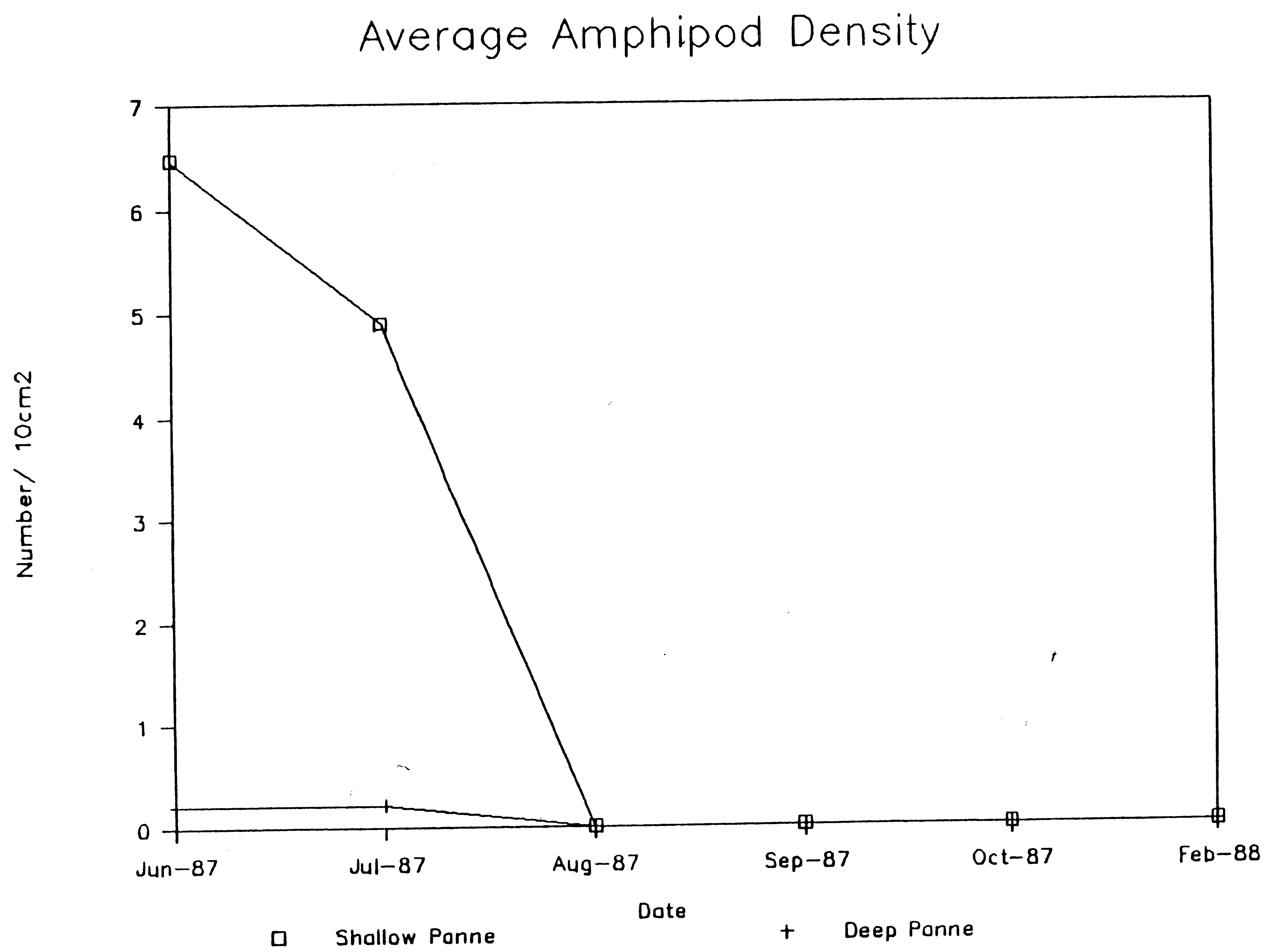

Average Amphipod Density
Number/ 10cm2
0
1
2
3
4
5
6
7
Jun–87
Jul–87
Aug–87
Sep–87
Oct–87
Feb–88
Date
Shallow Panne
Deep Panne

FIGURE 6

Average midge density for each sampling date in shallow and deep pannes.

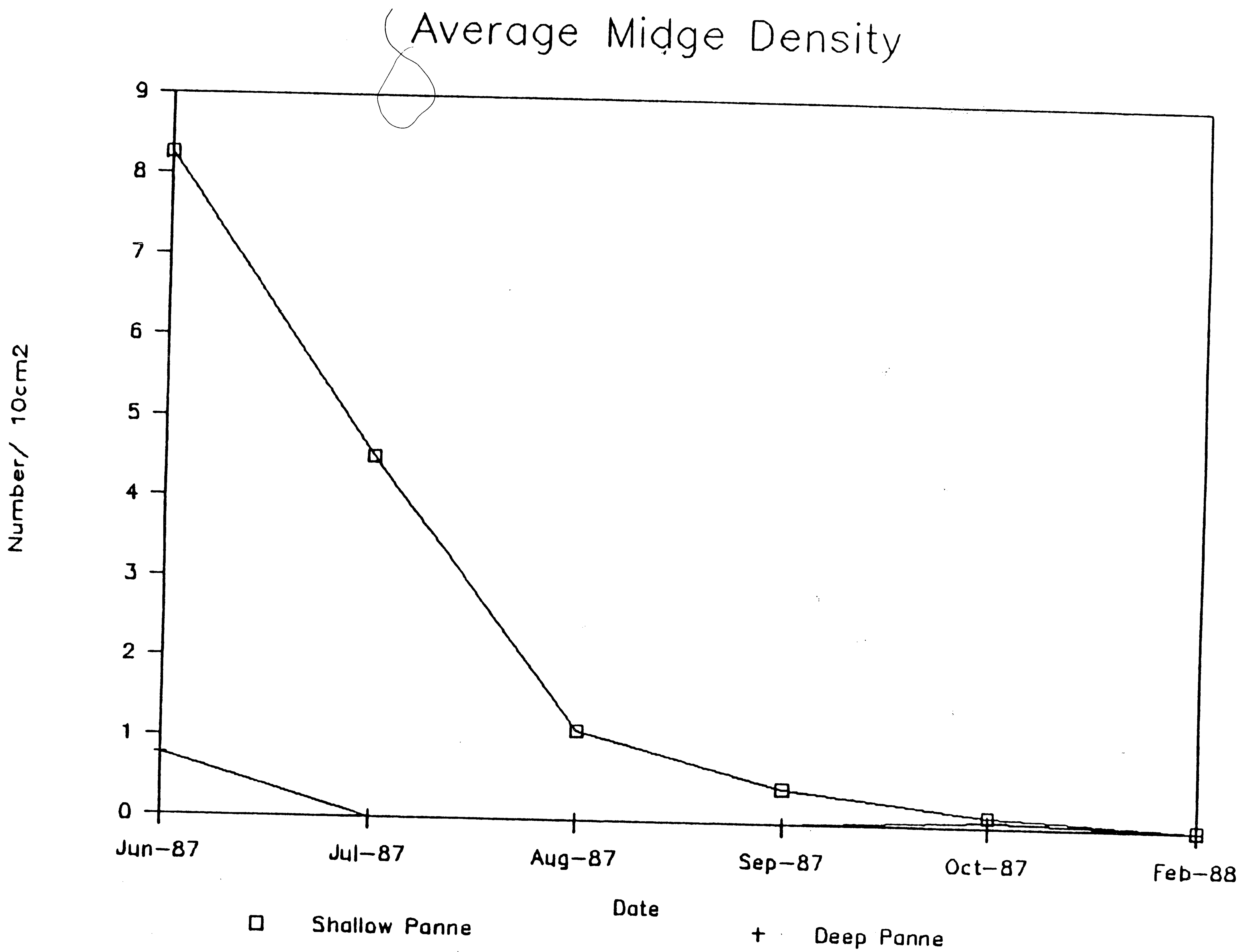
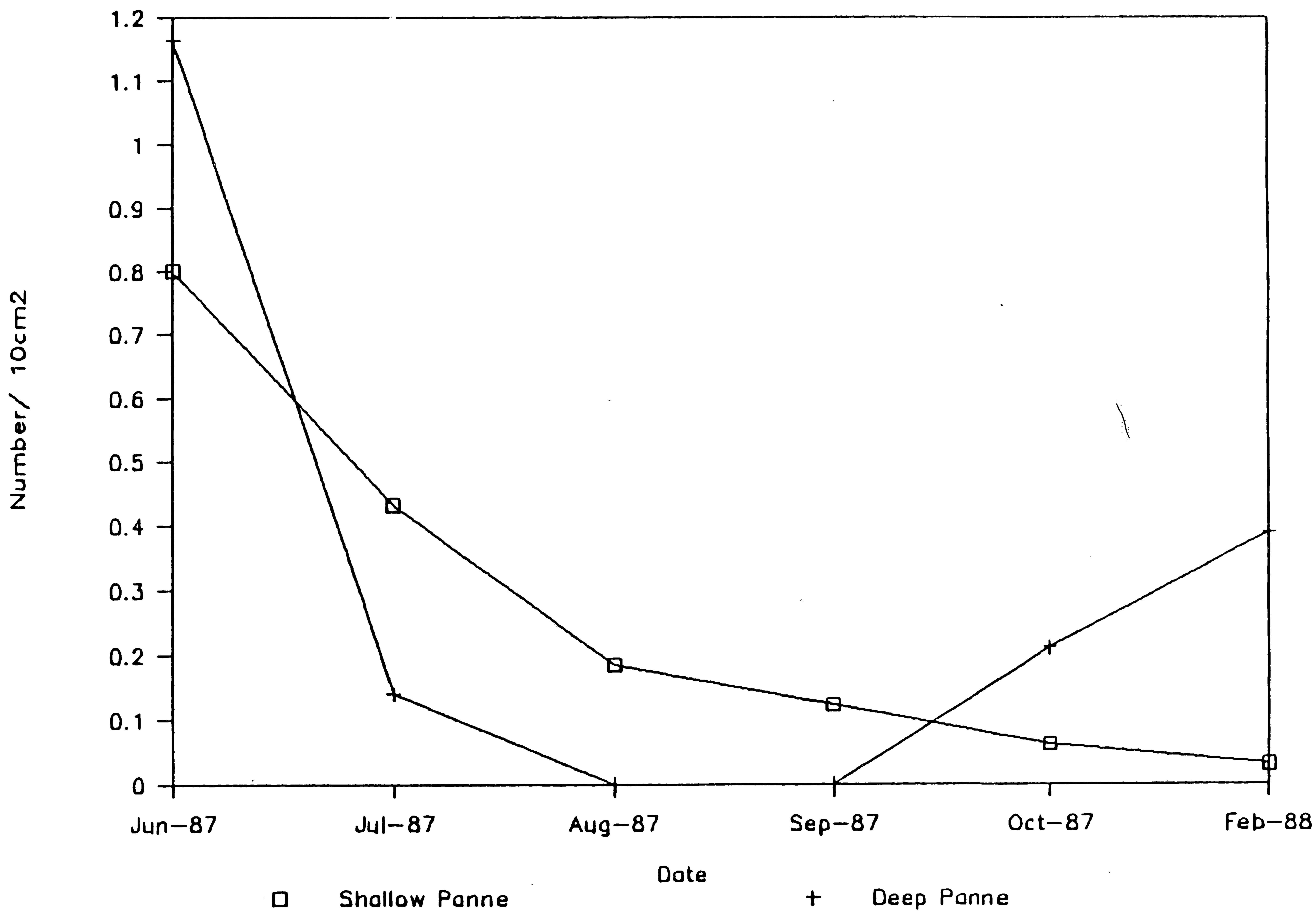

Average Midge Density
Number/ 10cm2
0
1
2
3
4
5
6
7
8
9
Jun-87
Jul-87
Aug-87
Sep-87
Oct-87
Feb-88
Date
Shallow Panne
Deep Panne

FIGURE 7

Average polychaete density for each sampling date in shallow and deep pannes.

Average Polychaete Density



pannes, at the 5% significance level. The average amphipod density in the shallow pannes reached a maximum level of $6.48/10cm^2$, whereas the maximum amphipod density in the deep pannes was only $0.21/10cm^2$, indicating a much higher amphipod population in the shallow pannes. The average midge density in the shallow pannes reached a maximum of $8.26/10cm^2$, while the maximum midge density in the deep pannes was only $0.77/10cm^2$. These figures show that the density of both midges and amphipods was approximately ten times greater in the shallow pannes than in the deep pannes. The polychaetes, (Family; Capitellidae) are statistically the same in both panne types, with an average maximum density of approximately $0.8/10cm^2$. A graph of the total numbers of organisms collected, (Figure 8) shows the same pattern, the level of amphipods and midges is much higher in the shallow pannes, and the level of polychaetes is the same.

Although there seems to be higher salinity and temperature in the shallow pannes (Figures 9 and 10) both the Wilcoxon Mann-Whitney U statictic, and Lord's test for two independent samples indicate that there is no difference in either salinity or temperature between the two types of panne.

Silt/Clay fractions were determined for the pannes to compare the two panne types (Table 3). Statistical analysis of these results using both the U statistic, and

FIGURE 8

Total number of polychaetes, amphipods, and midges collected in shallow and deep pannes over the entire course of the study.

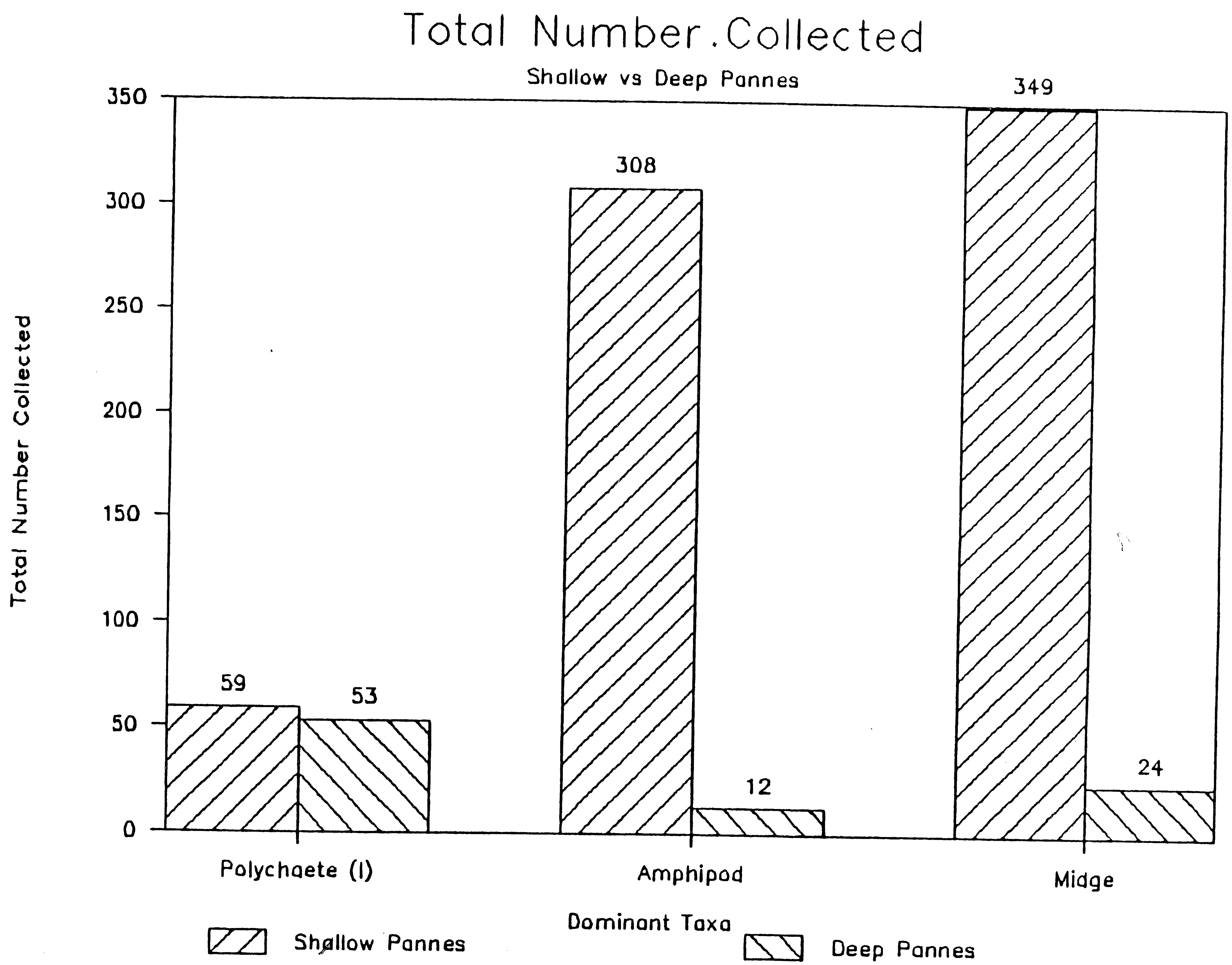

Total Number.Collected
Shallow vs Deep Pannes
350
300
250
200
150
100
50
0
Total Number Collected
308
349
59
53
12
24
Polychaete (I)
Amphipod
Midge
Dominant Taxa
Shallow Pannes
Deep Pannes

FIGURE 9

Average salinity values for each sampling date in shallow and deep pannes.

Average Salinity Values

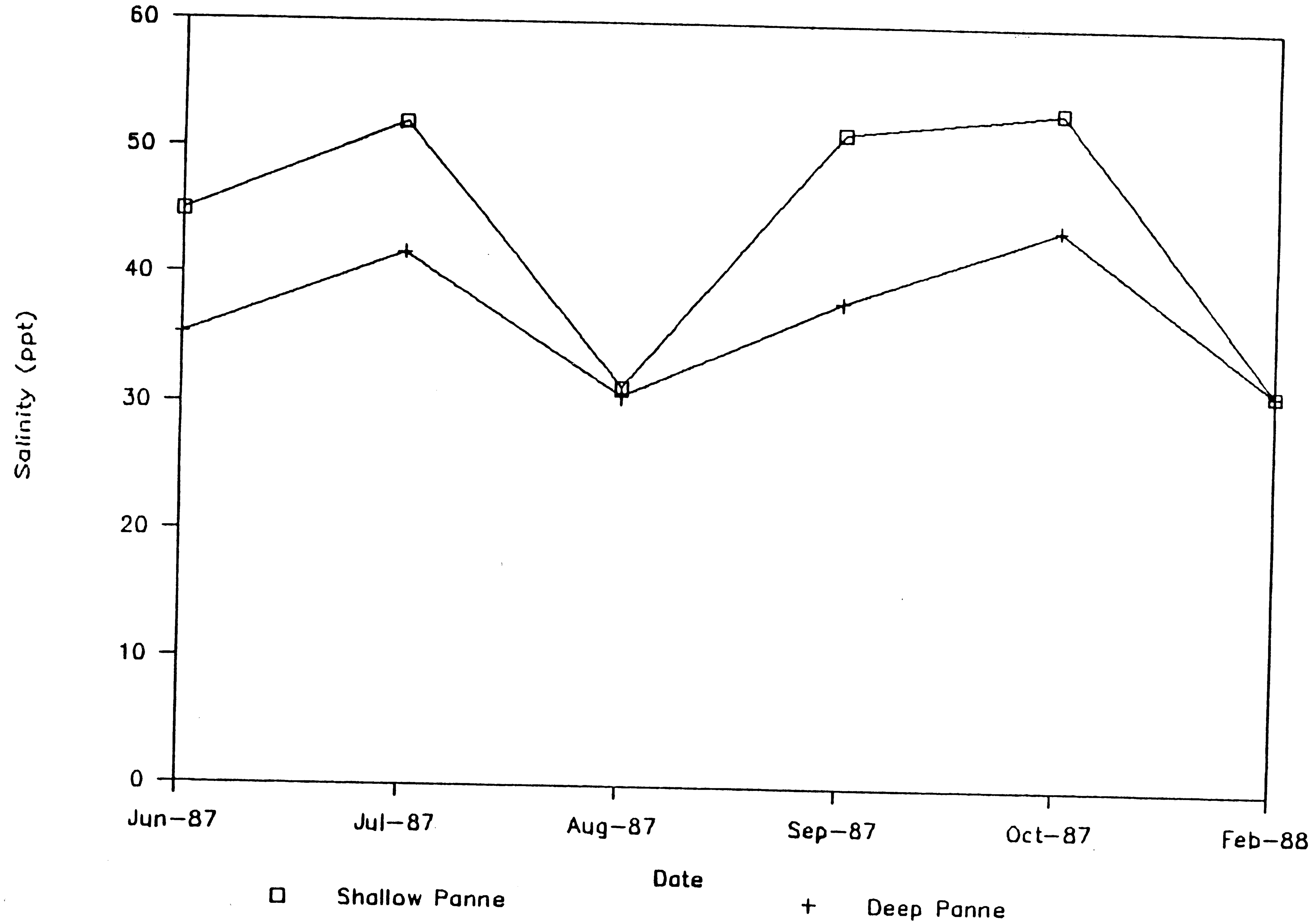


FIGURE 10

Average temperature values for each sampling date in shallow and deep pannes.

Average Temperature Values

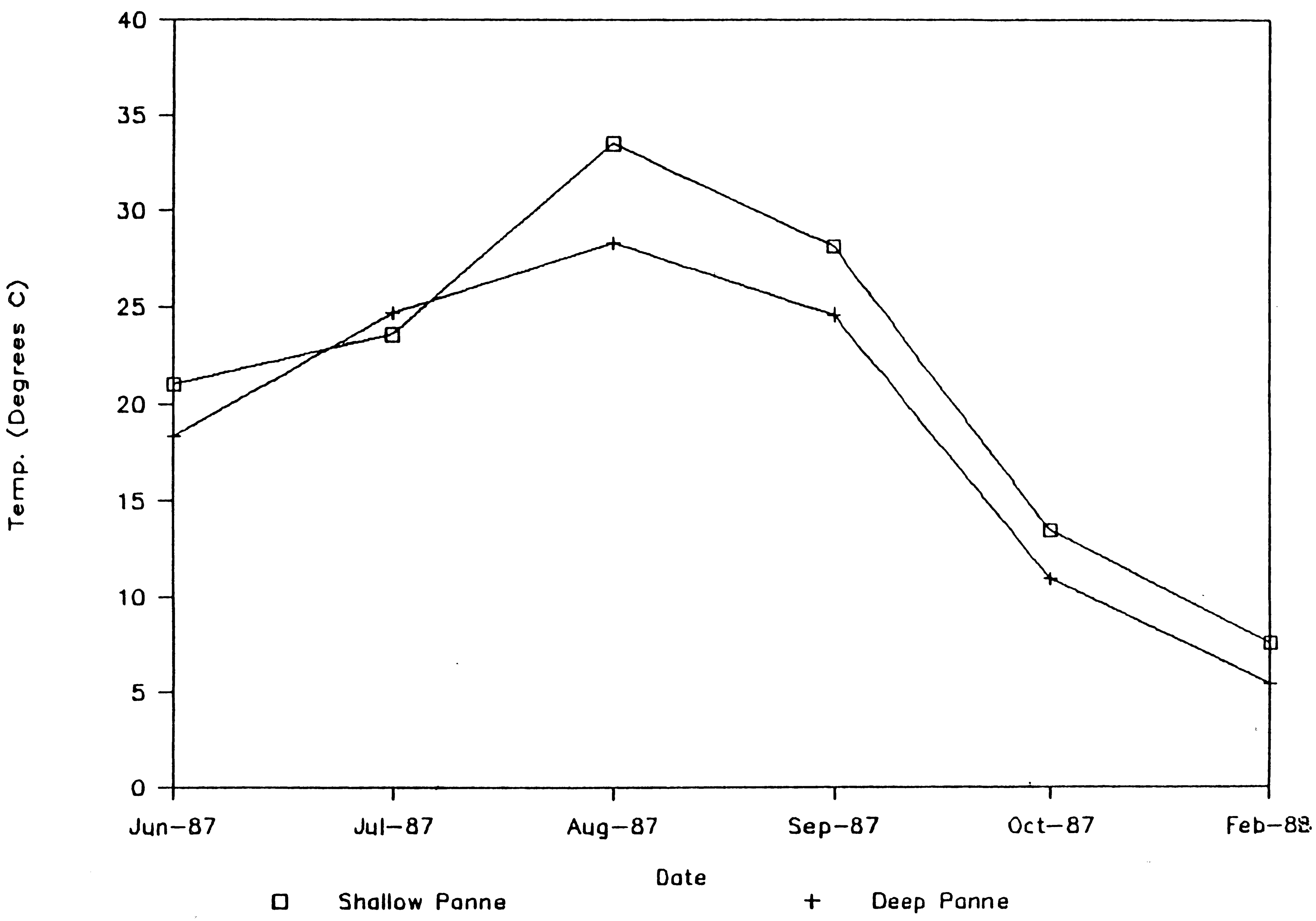


TABLE 3

Silt/clay fraction values for each panne. The high value of p indicates that there is no significant difference between the silt/clay fraction values for the two different types of panne.

Silt/Clay Fraction

Shallow Pannes		Deep Pannes	
1	21.2%	3	31.2%
2	37.1%	7	30.3%
4	33.1%	9	37.6%
5	24.3%	10	24.1%
6	41.2%	11	23.9%
8	22.7%	12	30.0%
14	20.1%	13	37.6%
15	29.8%		

p=.451

Lord's test for two independent samples, shows no difference between the two types of pannes.

Simple linear regressions were performed using the faunal numbers as dependent variables, and the salinity and temperature values as independent variables. A total of twelve regressions were performed, to see if there was any correlation between any of the faunal variation and the variation in salinity and temperature. None of the regressions showed a relationship between any of the factors tested. All of the R-squared values were below 10%. Which indicates no correlation between the fauna levels, and either temperature, or salinity. Two regressions were also performed to see if there was any correlation between temperature and salinity, and there was not, with all of the R-squared values being below .1%.

Patterns

Figures 11 and 12 show an interesting pattern. These figures show the mean data for the dominant midge, and the dominant polychaete in the deep pannes. The pattern is interesting because there are peaks for these two organisms in both the Spring and the Fall. This differs from all organsims in the shallow pannes, and from the polychaete in the deep panne, all of which

FIGURE 11

Average midge data in the deep pannes for each sampling date.

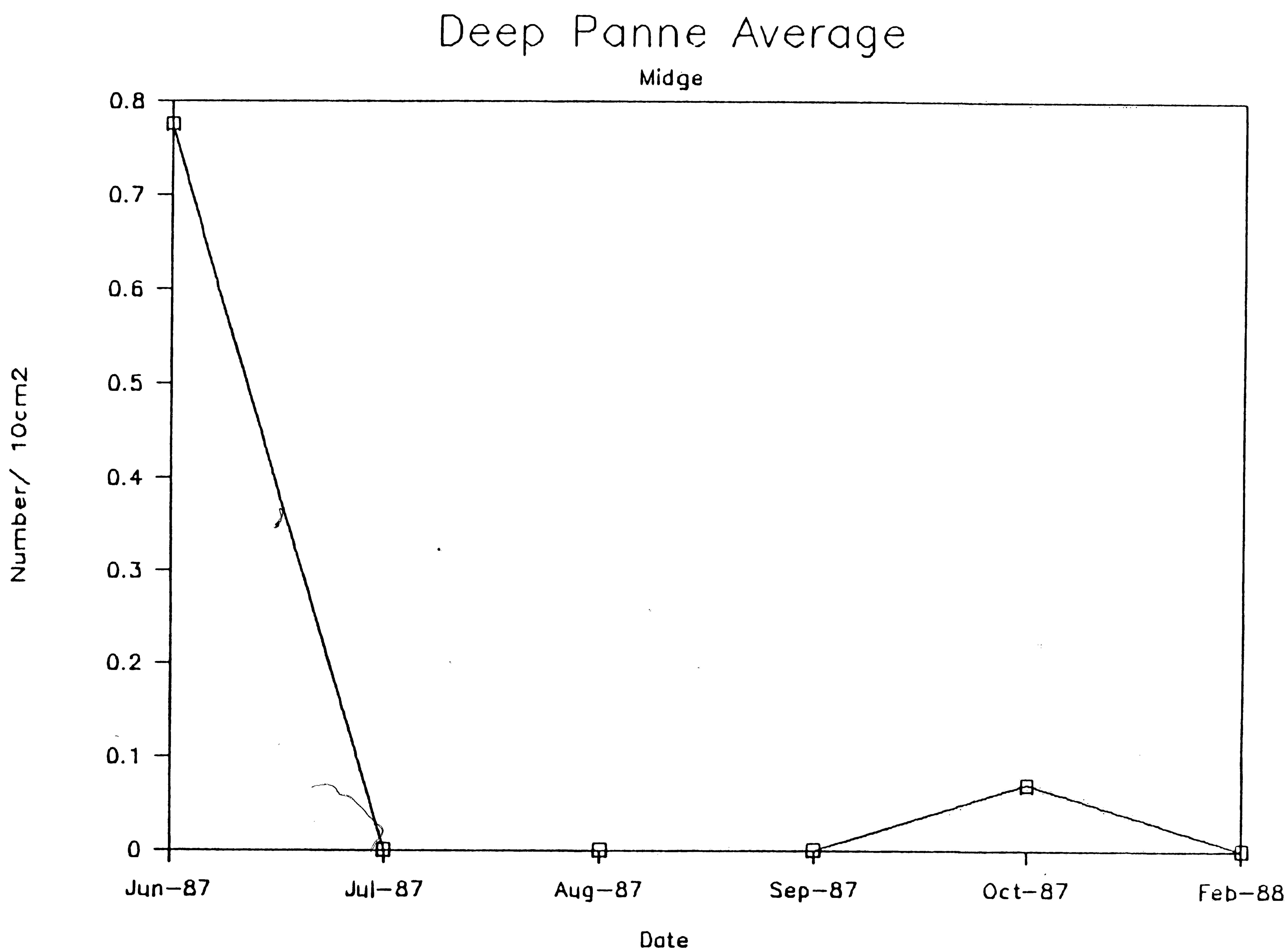
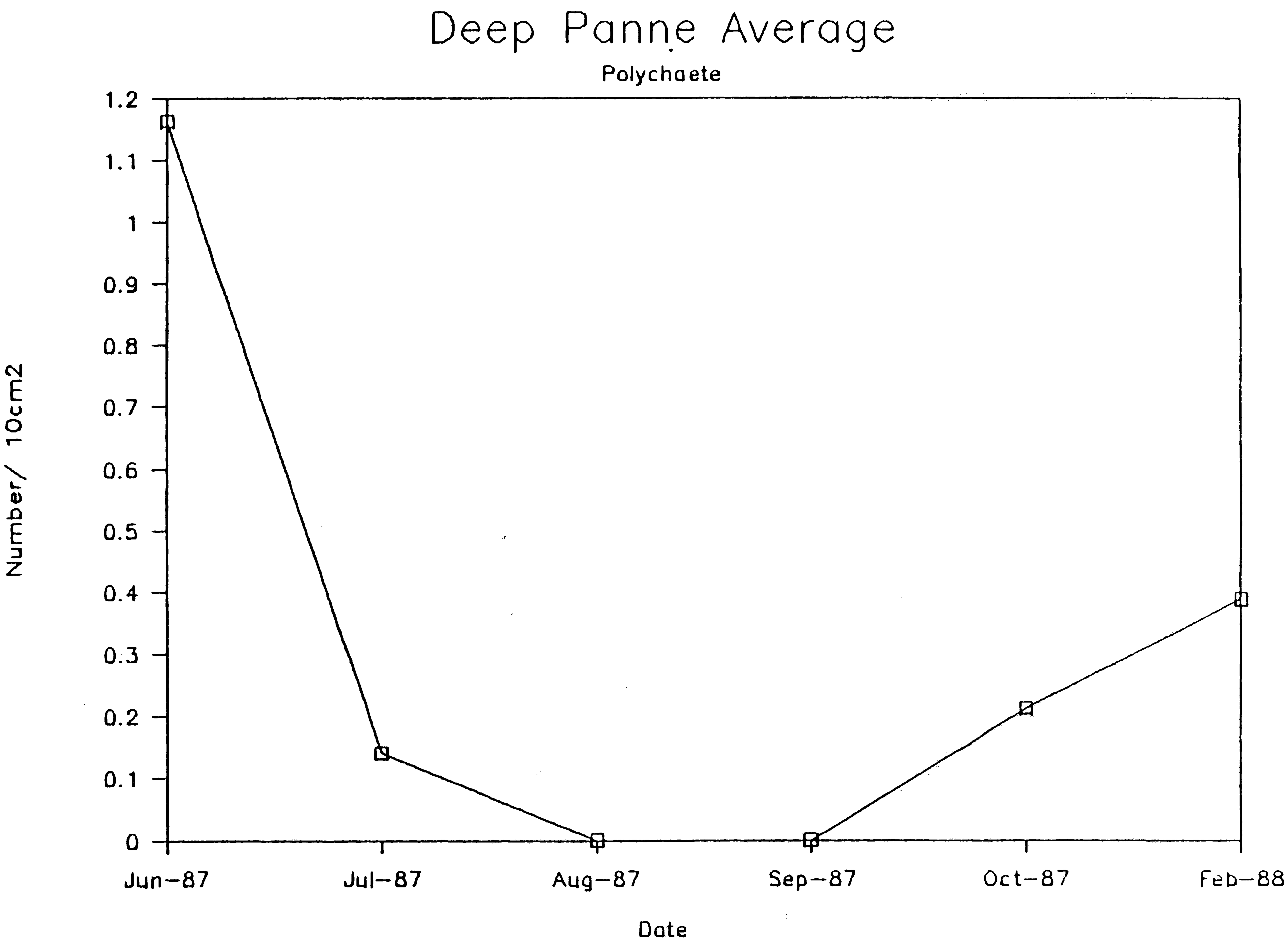

Deep Panne Average
Midge
Number/ 10cm2
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Jun-87
Jul-87
Aug-87
Sep-87
Oct-87
Feb-88
Date

FIGURE 12

Average polychaete data in the deep pannes for each sampling date.


Deep Panne Average
Polychaete
Number/ 10cm2
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Jun-87
Jul-87
Aug-87
Sep-87
Oct-87
Feb-88
Date

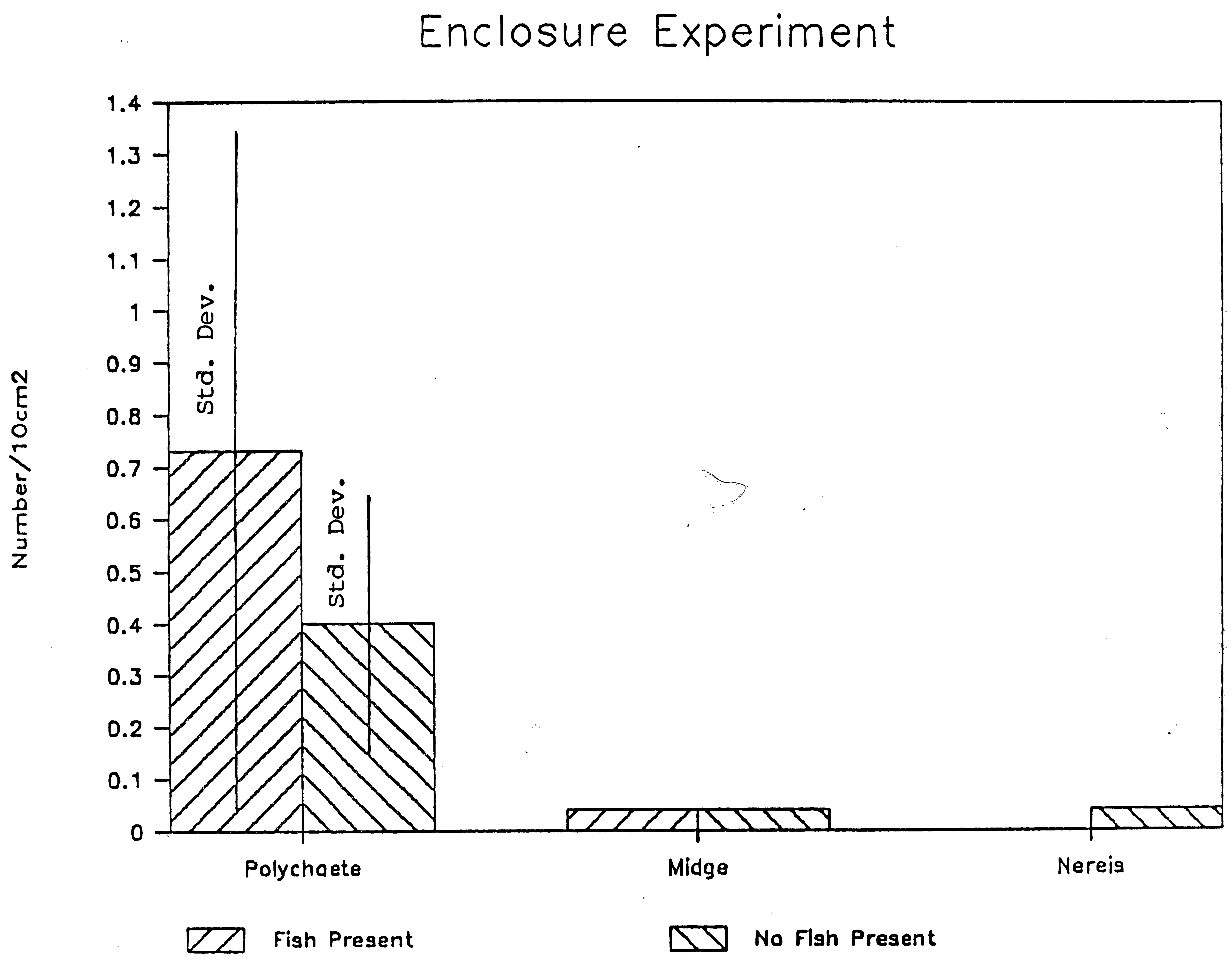
showed peaks in the spring with a tapering off for the rest of the year.

Enclosure Experiment

Figure 13 shows the results of the enclosure experiment. The only organism whose density may have been effected by the experiment was the polychaete (Family: Capitellidae). The density of polychaetes in the enclosure with fish present was $0.74/10cm^2$, whereas the level in the enclosure with no fish present was $0.4/10cm^2$. However, this is not a significant difference. The standard deviations for these two densities are 1.35 for the enclosure with fish present, and 0.61 for the enclosure with no fish present, indicating a need for a larger sample size. The other two organisms present in the experiment were the midge (Family; Ephydridae), and the polychaete, Nereis sp. that was abundant in the tidal creeks. Neither the midge nor Nereis, showed any difference between the two types of enclosure, fish present, or no fish present. Possible explanations for this will be discussed in the next section.

FIGURE 13

Results of enclosure experiment showing densities of organisms in enclosures with and without fish. There were no significant differences between enclosures for any of the organisms.



Enclosure Experiment
Number/10cm2
1.4
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Std. Dev.
Std. Dev.
Polychaete
Midge
Nereis
Fish Present
No Fish Present

DISCUSSION

The results of the comparison between the pannes and the tidal creeks suggest that there is little overlap between these two macrobenthic communities. The three dominant panne macrobenthic organisms are not present on the tidal creeks at all, and the dominant tidal creek organisms are present in the pannes in very low densities (Table 2a). These results are not surprising, since these areas are very different physically. The tidal creeks resemble the bay environment much more closely than the pannes. They do not have that same flucuations in temperature, salinity, and oxygen levels (Master 1989) that exist in the pannes. Because they are flooded only once or twice a month instead of twice a day, the pannes present a much harsher environment. Salinity levels sometimes reach a maximum of 75 0/00, while the tidal creek salinity levels never go above that of the bay, which peaks at approximately 32 0/00 (Daiber 1982, Teal 1962). Temperatures of 35 degrees C were recorded in the pannes while the temperature in the tidal creeks was never measured over 23 degrees C. This leads to a greater variability in the physical parameters, which would tend to change the structure of the community (Paine 1966).

These results are supported when compared with data from other salt marsh studies. The tidal creek data are very similar to that of the creek banks or the low marsh area in Dorges' (1977), study of Sapelo Island, Georgia. The creek banks were dominated by a bivalve, the oyster (*Crassostrea virginica*), a gastropod, the mud snail (*Nassarius obsoletus*), and a large predatory polychaete, (*Diopatra cuprea*). The low marsh areas were dominated by two bivalves, the ribbed mussel (*Modiolus demissus*), and *Crassostrea virginica*. In the current study, the creeks were dominated by *Nassarius obsoletus*, and the polychaete *Nereis* sp.. *Nassarius* was dominant in Dorge's study, and *Nereis* is a predatory polychaete as is *Diopatra*. The other organism these two studies had in common was *Modiolus demissus*. This shows faunal similarity between two marsh areas that are widely separated geographically.

Although there are no pannes in Dorges' study, the areas that he describes as the barrens, and the high marsh are the areas where the pannes occur in the New Jersey salt marsh. The only benthic organism that was present in these areas in the Sapelo Island study was the fiddler crab, *Uca pugnax*. While I did not include *Uca* in the current study, I did note that it was found only along the banks of the tidal creeks. In the pannes there were three dominant organisms, the polychaete (Family; Capitellidae), which I believe to be a new species, the midge (Family; Ephydridae), and the amphipod, *Gammarus* *palustris*. None of these three organisms, or any organisms from the same phyla, were present in the high marsh area on Sapelo Island. Obviously the pannes are just as different from Dorges' intertidal area, and upper marsh area, as they are from the tidal creeks which exist in the same marsh.

When the panne data are compared to those of other marsh studies, some very interesting correlations are revealed. In his work on lower Marshes in the Delaware area, Daiber (1982) found phyla similar to those found in the panne study; insects, polychaetes, and crustaceans. However, here is where the similarities end. In the pannes each of these groups is represented by only a single species, while Daiber showed several species of each. It is well known that species richness is a good indicator of health or stressfulness of an environment (Paine 1966, Sanders 1968). Low species diversity occurs in high stress environments, and the pannes are a good example of this. The pannes are similar to the lower aquatic areas of the marsh in their type of environment and as a result have the same taxonomic groups represented. However, the pannes experience much greater flucuations in salinity, temperature, and dissolved oxygen, which leads to a much lower species richness.

The same pattern is seen when the pannes are compared to Teal's (1962) study of Sapelo Island, Georgia. The same taxonomic groups occur in the Sapelo Island marsh, crustaceans, polychaetes, and dipteran larvae and the maximum densities are similar. Teal records dipteran larvae with a maximum density of $10/10cm^2$, and _Capitella capitata_, a polychaete of the same family as those in the pannes, with a maximum density of $13/10cm^2$. In the pannes midge densities reached a maximum of $8.3/10cm^2$, and polychaetes a maximum of $1.2/10cm^2$. The difference arises when species diversity in these groups is examined. The lower marsh in the Sapelo Island study has a considerably greater number of species from each of these groups than do the pannes.

An obvious comparison can be made with the Nova Scotia study of Bromley and Bleakney (1979). This is a study of "pannes" in a _Spartina patens_ marsh bordering the Bay of Fundy. Although the area of the marsh is comparable, the pannes are not the same since they flood only during the Spring of the year, so they are isolated for much longer periods of time, and the salinities range from 20.5 to 39 0/00, whereas the NJ pannes flood at least every month, and the salinities range from 30 to 74 0/00. The marshes are also dominated by two different species of grass, Cordgrass, (_Spartina alterniflora_), in NJ, and Salt Hay, (_Spartina patens_), in Nova Scotia. The Nova Scotia pannes showed a much greater species diversity than the NJ pannes. There were 5 species of snails, 7 species of bivalves, 14 species of polychaetes, 10 species of crustaceans, and 4 species of insects, all of which were collected in numbers high enough to suggest that they were permanent residents of the pannes. In the NJ pannes there was only 1 species of polychaete, 1 species of crustacean, and 1 species of insect that were permanent residents of the pannes. Because of the flooding regimes and the salinity range, the NJ pannes are a much more stressful environment than those in Nova Scotia, and this is reflected in the amount of species diversity.

Figures 5 and 6 show that the amphipods and the midges have a peak of activity in the spring, taper off in the Summer, and virtually disappear in the fall and winter. These results match those of the preliminary investigations which showed little activity for these two organisms in the winter. Figure 7 shows that the polychaetes are present all year round, with a peak in the spring, and a low point in the late summer. This is also supported by the preliminary investigation, which showed that the polychaetes were the only species present in the Winter.

Figures 5, 6, and 7, show the mean data for all three dominant panne organisms for each sampling date, divided by shallow and deep pannes. When these data were examined statistically using the Wilcoxon Mann-Whitney U statistic, there was no difference between the shallow or deep pannes for any of the three dominant species. However, this test can be greatly affected by a large number of zeros, and because of the ranking system used, it does not take into account the relatively large difference in the means for some of the data. To correct for this, the data were tested again, using Lord's test for two independent samples, which takes into account the means of the samples, and uses the range of the data as part of the test statistic. This test showed a clear difference between the populations of amphipods, and midges in the shallow and deep pannes at the 5% level. The polychaetes were not significantly different according to both tests. Linear correlations were performed on all of the dominant faunal mean data, and the temperature and salinity data. This was a preliminary attempt to see if there may have been any relationship between faunal levels, and either of these physical factors. While a correlation does not imply cause, a negative result could imply no relationship, and a positive result would be reason for further investigation. Since there was no correlation between any of the faunal levels, and any of the physical parameters measured, these physical factors do not seem to be the main factors involved in determining faunal levels during any of the times sampled.

The total numbers graph (Figure 8) shows that there is a difference in the standing crops between the shallow and deep pannes. This difference is the opposite of what was expected. Since the shallow pannes have a greater flucuation in temperature, and salinity, one might expect that fewer organisms would be present. This does not seem to be the case. The shallow pannes have more amphipods, and midges, and approximately the same number of polychaetes as the deep pannes. There are several possible reasons for this. Both groups (amphipods and midges) may use the dense mat of rhizomes in the shallow pannes (Borowsky and Borowsky 1987, Rees 1975, Van Dolah 1978). These rhizomes may also provide food for these organisms.

This result should not be surprising. Although, the measured sediment parameters show no difference between the two types of pannes, the presence of <u>Spartina</u> rhizomes in the shallow pannes, and their absence in the deep pannes is an obvious physical difference. This difference may correlate with the kind of sediment differences usually found in benthic environment, which is best illustrated by muddy vs. sandy sediments. Sandy sediments are usually dominated by molluscs and crustaceans, and muddy sediments are often dominated by polychaetes (Sanders 1958,1960). These differences are caused by the effects the sediments have on benthic organisms. Muddy sediments afford a poor attachmemt substrate for sessile organisms, and have a tendency to clog the filtering or gill appartus of many organisms (Rhoads and Young 1970, Sanders 1958) The species of amphipod found in the pannes is known to live in Spartina stems, and may be able to hide in the rhizomes present in the shallow pannes (Rader 1984, Rees 1975, Van Dolah 1978).

The higher organic content of the sediment in the deep pannes represents another major difference (Itzkowitz and Guida 1983). A higher organic content is typically present in muddy sediments and this is usually an advantage to deposit feeders, such as some bivalves and polychaetes (Teal 1962, Sanders 1958). However, in the pannes the only likely deposit feeder is the polychaete (Family; Capitellidae), which is the only one of the three dominant organisms which is common to both types of panne. Since the two dominant species which do differ, the midges and the amphipods, are not deposit feeders, this explanation probably does not apply to them.

I believe that one likely explanation for the differences between pannes lies with the sheepshead minnow, *Cyprinodon variegatus*, and the mummichog, *Fundulus heteroclitis*, that inhabit the deep pannes.

These fish are known to prey on midges and amphipods (Clymer 1978, Kneib and Stiven 1982) and this may account for their absence from these pannes.

An attempt was made to examine this question with the enclosure experiment. The results here were not conclusive. During the duration of the experiment, there was no change in the number of midges or amphipods, the organisms that were suspected of being preyed upon by the fish. One possible explanation for this is that the experiment must be conducted in the spring when the densities of these organisms is on the rise instead of the fall when the numbers are already decreasing. There was one difference noted in the experiment, the number of polychaetes increased in the enclosure that held fish. There are several possible reasons for this. The polychaetes may feed on the fecal pellets of the fish and therefore may be attracted to these enclosures, or, the fish may prey on the polychaete Nereis which may in turn feed on the dominant polychaete (Family: Capitellidae). One of the few times Nereis was collected in a panne was in an enclosure with no fish, and no dominant polychaetes, the numbers, however, were too small to be statistically significant.

The first objective of this study was to compare the pannes to the tidal creeks around them (Figure 4). There seems to be almost no overlap between the macrobenthic species in the pannes and the tidal creeks. There also seems to be a difference between the shallow pannes and the deep pannes. Since the physical parameters do not differ statistically, the answer most likely is a result of biological interaction. The obvious possibility is bioturbation. Bioturbation occurs when deposit feeders disturb the sediment, and thereby effect other organisms which may seek to settle in this area, by choking out the larval stages (Levinton 1977, Rhoads and Young 1970, Yingst and Rhoads 1980). The only dominant organism which is found in both types of panne is the polychaete, (Family; Capitellidae). This organism is a likely candidate for the bioturbation. Although, this polychaete is present alongside the other two dominant organisms in the shallow pannes, the same affect is not seen. The rhizomes present in the shallow pannes, the fish present in the deep pannes, or a combination of these two may be the reason. A description of the dominant species in the panne macrofauna has been developed, and part of the cycle for one year has been recorded.

This study was designed to examine the panne macrobenthos, and the differences between the panne types, and the pannes and the tidal creeks. Studying the macrobenthos helped to maximize these differences. With this preliminary investigation completed, the next step should involve the remaining components of the benthic community, and their subsequent impact on the panne food chain. This would involve fish stomach contents analysis in the pannes, to determine whether or not they are eating a significant fraction of the benthic population. Ideally, this study would be linked with a similar study of the plankton and algae present in the pannes. This could help determine the place of the pannes in the entire salt marsh food chain, and help gauge their importance in terms of production. This study could have been improved by taking more samples, to strengthen the statistical tests performed on the data, however, the constraints of time and space for sampling prevented this. If I were to do this study over again, I would start earlier in the spring to try to determine when the midges and amphipods first appeared in the pannes, and to try to determine their origin.

Speculation

I believe that the dominant polychaete (Family: Capitellidae) may play an important role in the formation and the ecology of these pannes. Levinton (1977) shows that other deposit feeders, can play an important role in the sediment conditions of an area, both because of the breakdown of the sediment and the depositing of fecal pellets. His experimental results are very similar to the condition of the sediment in the deep pannes, and I suspect that the dominant polychaetes here have a similar affect. Other studies also show a similar effect on production and diversity (Rhoads and Young 1970, Yingst and Rhoads 1980, and Warwick 1980).

It is also possible that the shallow pannes are younger than the deep pannes and may not yet have had the chance to break down to the point of soft sediment as the deep pannes have. Two weaknesses to this theory are the absence of any pannes that seem to be in an intermediate state, and the _Spartina_ rhizomes, which are either present or not, with no gradual disappearance. It may be that a storm, or unusually high tide is needed to kill the rhizomes, and allow the polychaetes to work on breaking down the sediment.

I also suspect that the polychaetes may be important in the nutrient cycle of the marsh. The detritus which falls into the pannes may be ingested by the polychaetes, and formed into the fecal pellets which are so abundant in the deep pannes. These pellets may make these nutrients much more available as the basis of the food chain. This would be a system analogous to that of the earthworm, which consumes leaf litter, and contributes to the availability of nutrients in the soil. Interestingly, the dominant polychaete in the pannes does resemble the earthworm to a remarkable degree, both physically, and in the way it tunnels throuth the sediments. It was these observations in the laboratory which first led me to make the comparison.

BIBLIOGRAPHY

Bell, S.S. 1980. Meiofauna-Macrofauna interactions in a high salt marsh habitat. Ecological Monographs. 50(4):487-505.

Bell, S.S., and B.C. Coull. 1978. Field evidence that shrimp predation regulated meiofauna. Oecologia. 35:141-148.

Bell, S.S., and B.C. Coull. 1980. Experimental evidence and a model for juvenile Macrofauna-Meiofauna interactions. In: K.R. Tenore, and B.C. Coull (Eds.) Marine Benthic Dynamics. University of South Carolina Press, Columbia, SC. pp.179-192.

Borowsky, B., and R. Borowsky. 1987. Feeding by the salt marsh amphipod, Gammarus palustris, on Ulva and Enteromorpha. Abstract. American Zoologist. 27(4):55A #285

Bousfield, E.L. 1973. Shallow Water Gammaridean Amphipoda of New England. Comstock Publishing Associates, Cornell University Press, Ithaca, NY. 312pp.

Bromley, J.E.C., and S. Bleakney. 1979. Taxonomic survey of benthic gauna in estuarine saltmarsh pools, Minas Basin, Bay of Fundy. Proceedings of the Nova Scotia Institute of Science. 29:411-446.

Clymer, J.P. 1978. The distributions, trophic activities and competitive interactions of three salt marsh killifishes (Pisces: Cyprinodontidae). Ph.D. Dissertation. Lehigh University. 281pp.

Cummings, E., and E. Ruber. 1987. Copepod colonization of natural substrates in a salt marsh pool. Estuarine, Coastal and Shelf Science. 25:637-645.

Daiber, F.C. 1982. Animals of the Tidal Marsh. Van Nostrand Reinhold Company, New York. 422pp.

Dorges, J. 1977. Marine macrobenthic communities of the Sapelo Island, Georgia region. In: B.C. Coull (Ed.) Ecology of Marine Benthos. University of South Carolina Press, Columbia, SC. pp.399-421.

Fauchald, K. 1977. The Polychaete Worms: Definitions and Keys to the Orders, Families and Genera. Natural History Museum of Los Angeles County, Science Series. 28:1-190.

Fleeger, J.W., S.A. Whipple, and L.L. Cook. 1982. Field manipulations of tidal flushing, light exposure and natant macrofauna in a Louisiana salt marsh: Effects on the meiofauna. Journal of Experimantal Marine Biology and Ecology. 56:87-100.

Gerlach, S.A. 1971. On the importance of marine meiofauna for benthos communities. Oecologia. 6:176-190.

Gosner, K.L. 1979. A Field Guide to the Atlantic Seashore. Houghton Mifflin Company, Boston. 329pp.

Haines, E.B. 1977. The origins of detritus in Georgia salt marsh estuaries. Oikos. 29:254-260.

Itzkowitz, M., and V. Guida. 1983. Technical Report: Marsh Trophic-Dynamics Project. The Wetlands Institute, Stone Harbor, New Jersey. 15pp.

Johnson, R.G. 1970. Animal-Sediment relations in shallow water benthic communities. Marine Geology. 11:93-104.

Kneib, R.T., and A.E. Stiven. 1982. Benthic invertebrate responses to size and density manipulations of the common mummichog, Fundulus heteroclitus in and intertidal salt marsh. Ecology 63:1518-1532.

Levinton, J.S. 1977. Ecology of shallow water deposit-feeding communities Quisset Harbor, Massachusetts. In: B.C. Coull (Ed.) Ecology of Marine Benthos. University of South Carolina Press, Columbia, SC. pp.191-227.

Master, T.L. 1989. The effects of prey characteristics and environmental structure on predator foraging strategies: A look at Snowy Egrets (Egretta thula) and their prey in salt marsh pannes. Ph.D. Dissertation, Lehigh University, Bethlehem, PA

Nolan, P.M. 1985. Variability and assessment of pool area Cladophora cover, biomass and production in a Northern Massachusetts salt marsh. Abstract. Estuaries 7(2B):25A #62.

Nixon, S.W., and C.A. Oviatt. 1973. Ecology of a New England salt marsh. Ecological Monographs. 43:463-498.

Nixon, S.W. 1980. Between coastal marshes and coastal waters - a review of twenty years of speculation and research on the role of salt marshes in estuarine productivity and water chemistry. In: P. Hamilton and K.B. MacDonald (Eds.) Estuarine and Wetland Processes with Emphasis on Modeling. Plenum Press N.Y. pp.438-525.

Odum, E.P. 1980. The status of three ecosystem level hypotheses regarding salt marsh estuaries: Tidal subsidy, outwelling, and detritus-based food chains. In: V.S. Kennedy (Ed.) Estuarine Perspectives. Academic Press NY. pp.485-496.

Paine, R.T. 1966. Food web complexity and species diversity. American Naturalist. 100:65-75.

Peterson, B.J., and R.W. Howarth. 1987. Sulfur, carbon and nitrogen isotopes used to trace organic matter flow in the salt-marsh estuaries of Sapelo Island, Georgia. Limnology and Oceanography. 32:1195-1213.

Rader, D.N. 1984. Salt-marsh benthic invertebrates: Small-scale patterns of distribution and abundance. Estuaries 7(4A):4133-420.

Rees, C.P. 1975. Life cycle of the amphipod Gammarus palustris. Estuarine and Coastal Marine Science. 3:413-419.

Rhoads, D.C., and D.K. Young., 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. Journal of Marine Research. 28:150-178.

Sanders, H.L. 1958. Benthic studies in Buzzard's Bay: I. Animal-Sediment relationships. Limnology and Oceanography. 3:245-258.

Sanders, H.L. 1960. Benthic studies in Buzzard's Bay: III. The structure of the soft bottom community. Limnology and Oceanography. 5:138-153.

Sanders, H.L., 1968. Marine benthic diversity: A comparative study. American Naturalist 102:243-282.

Short, F.T., and C.A. Short. 1984. The seagrass filter: Purification of estuarine and coastal waters. In: V.S. Kennedy (Ed.) The Estuary as a Filter. Academic Press NY. pp.395-414.

Siebert, J.R., and R.J. Naiman, 1980. The role of detritus and the nature of estuarine ecosystems. In: K.R. Tenore, and B.C. Coull (Eds.) Marine Benthic Dynamics. University of South Carolina Press, Columbia, S.C. pp.311-324.

Snedecor, G.W., and W.G. Cochran, 1980. Statistical Methods. The Iowa State University Press, Ames, Iowa. 507pp.

Soil Survey Staff. 1951. Soil Survey Manual, US. Department of Agriculture Handbook. 18:1-503.

Teal, J.M., 1962. Energy flow in the salt marsh ecosystem of Georgia. Ecology. 43:614-624.

Teal, J., and M. Teal. 1969. Life and Death of the Salt Marsh. Ballantine Books, New York. 274pp.

Van Dolah, R.F. 1978. Factors regulating the distribution and population dynamics of the amphipod Gammarus palustris in an intertidal salt marsh community. Ecological Monographs 48:191-217.

Warwick, R.M., 1980. Population dynamics and secondary production of benthos. In: K.R. Tenore, and B.C. Coull (Eds.) Marine Benthic Dynamics. University of South Carolina Press, Columbia SC. pp. 1-24.

Wenner E.L. and H.R. Beatty 1985. Seasonal and spatial relationships of macrobenthos from coastal impoundment, tidal creek and salt marsh habitats. Abstract. Estuaries 8(2B):41A #101.

Yingst, J.Y., and D.C. Rhoads, 1980. The role of bioturbation in the enhancement of bacterial growth rates in marine sediments. In: K.R. Tenore, and B.C. Coull (Eds.) Marine Benthic Dynamics. University of South Carolina Press, Columbia, S.C. pp.407-422.

APPENDIX

This appendix contains graphs of all the raw data for the study. The first fifteen graphs are the raw macrobenthos density data for the fifteen study pannes. The next fifteen graphs are the raw temperature data for the pannes, and the last fifteen graphs are the raw salinity data for the pannes. The graphs are interpreted by first reading the heading. This indicates which panne the graph applies to, and whether it is a macrobenthos, temperature, or salinity graph. The macrobenthos graphs include all of the densities from that particular panne for the three dominant macrobenthic organisms, on the sampling date in each month. The temperature data were taken at the time of sampling, as were the salinity data. To find a particular datum just turn to the graph for that panne, in the correct section, macrobenthos, temperature, or salinity, and look at the information on the graph for that particular date.

Siebert, J.R., and R.J. Naiman, 1980. The role of detritus and the nature of estuarine ecosystems. In: K.R. Tenore, and B.C. Coull (Eds.) Marine Benthic Dynamics. University of South Carolina Press, Columbia, S.C. pp.311-324.

Snedecor, G.W., and W.G. Cochran, 1980. Statistical Methods. The Iowa State University Press, Ames, Iowa. 507pp.

Soil Survey Staff. 1951. Soil Survey Manual, US. Department of Agriculture Handbook. 18:1-503.

Teal, J.M., 1962. Energy flow in the salt marsh ecosystem of Georgia. Ecology. 43:614-624.

Teal, J., and M. Teal. 1969. Life and Death of the Salt Marsh. Ballantine Books, New York. 274pp.

Van Dolah, R.F. 1978. Factors regulating the distribution and population dynamics of the amphipod Gammarus palustris in an intertidal salt marsh community. Ecological Monographs 48:191-217.

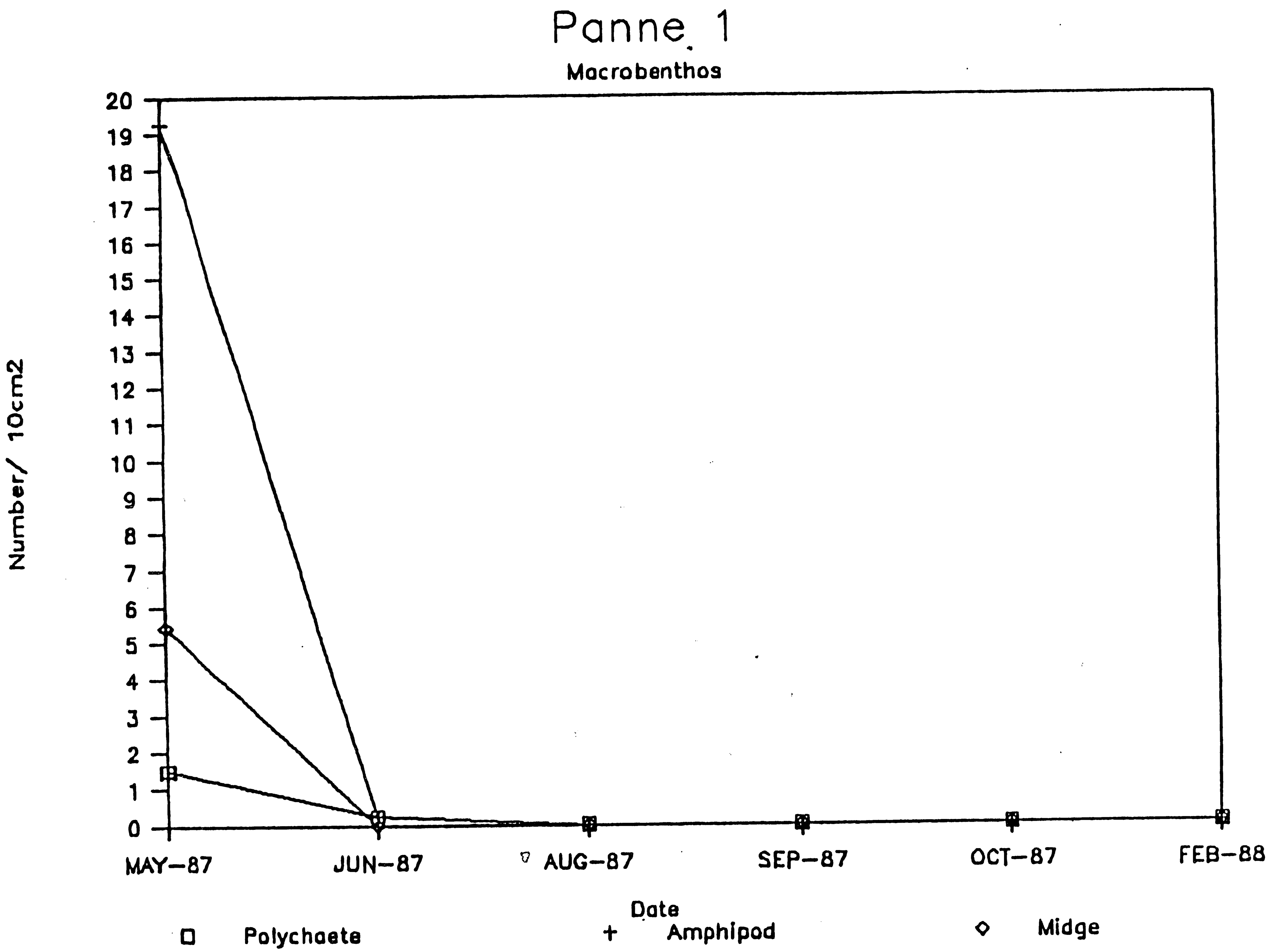
Warwick, R.M., 1980. Population dynamics and secondary production of benthos. In: K.R. Tenore, and B.C. Coull (Eds.) Marine Benthic Dynamics. University of South Carolina Press, Columbia SC. pp. 1-24.

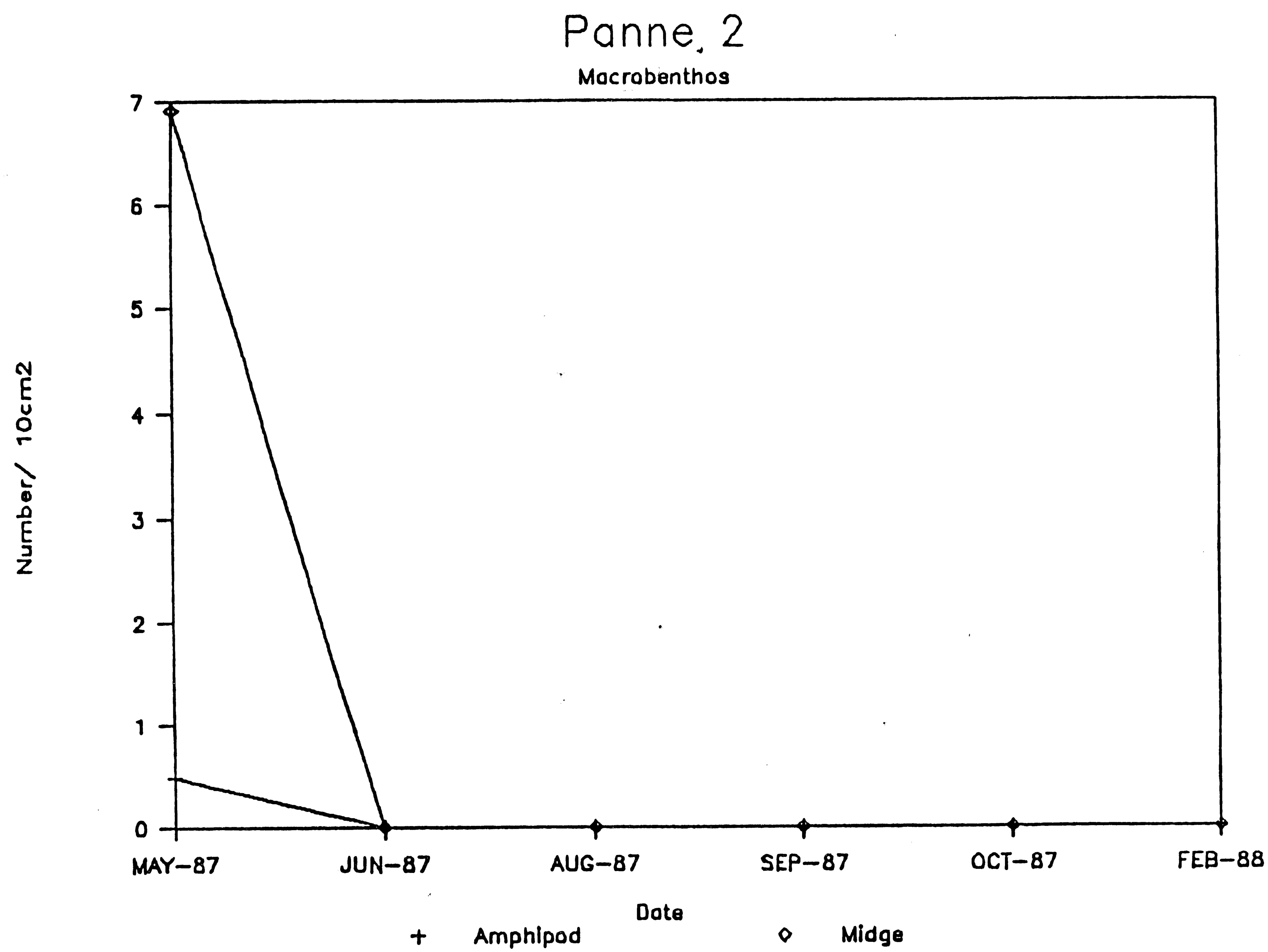
Wenner E.L. and H.R. Beatty 1985. Seasonal and spatial relationships of macrobenthos from coastal impoundment, tidal creek and salt marsh habitats. Abstract. Estuaries 8(2B):41A #101.

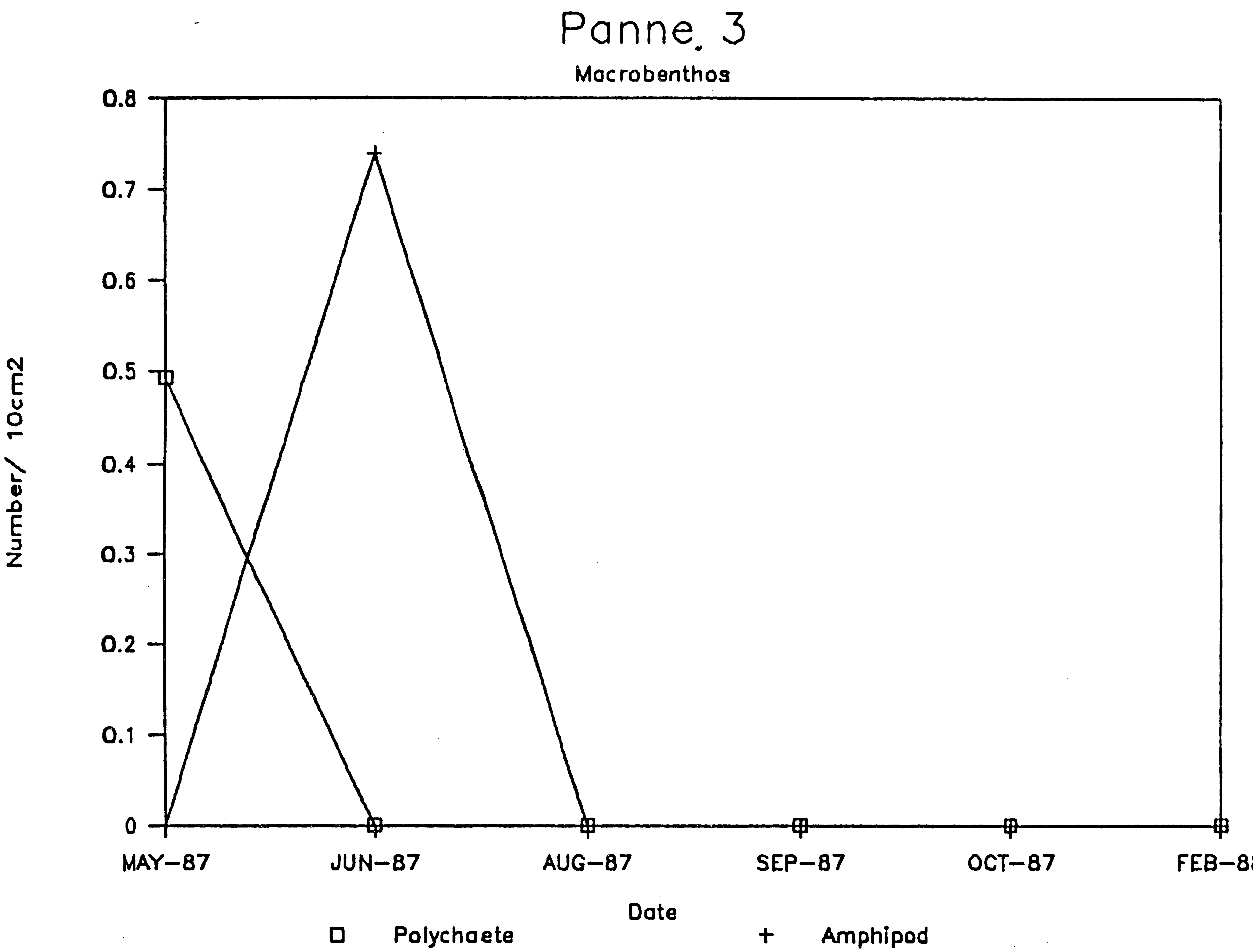
Yingst, J.Y., and D.C. Rhoads, 1980. The role of bioturbation in the enhancement of bacterial growth rates in marine sediments. In: K.R. Tenore, and B.C. Coull (Eds.) Marine Benthic Dynamics. University of South Carolina Press, Columbia, S.C. pp.407-422.

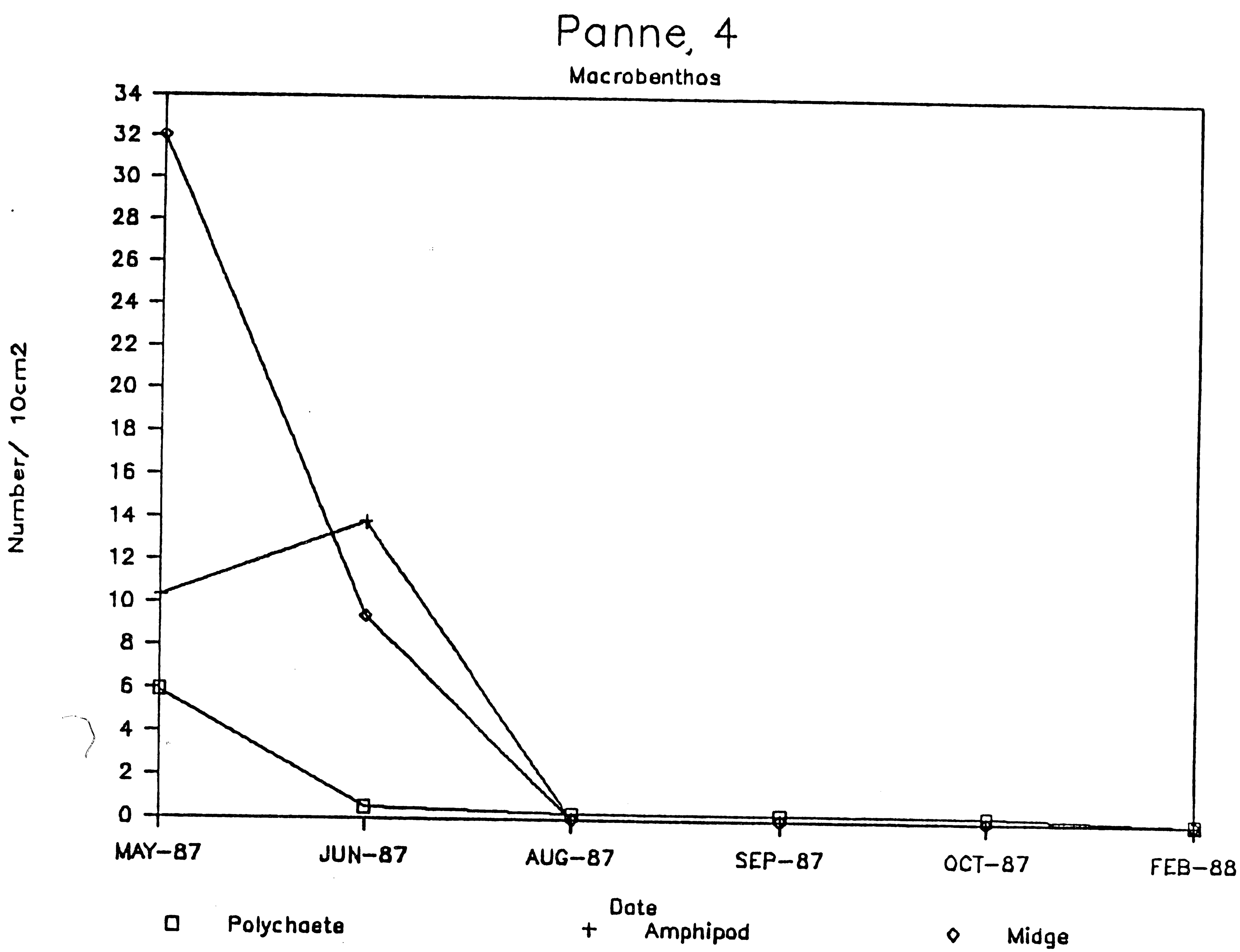
APPENDIX

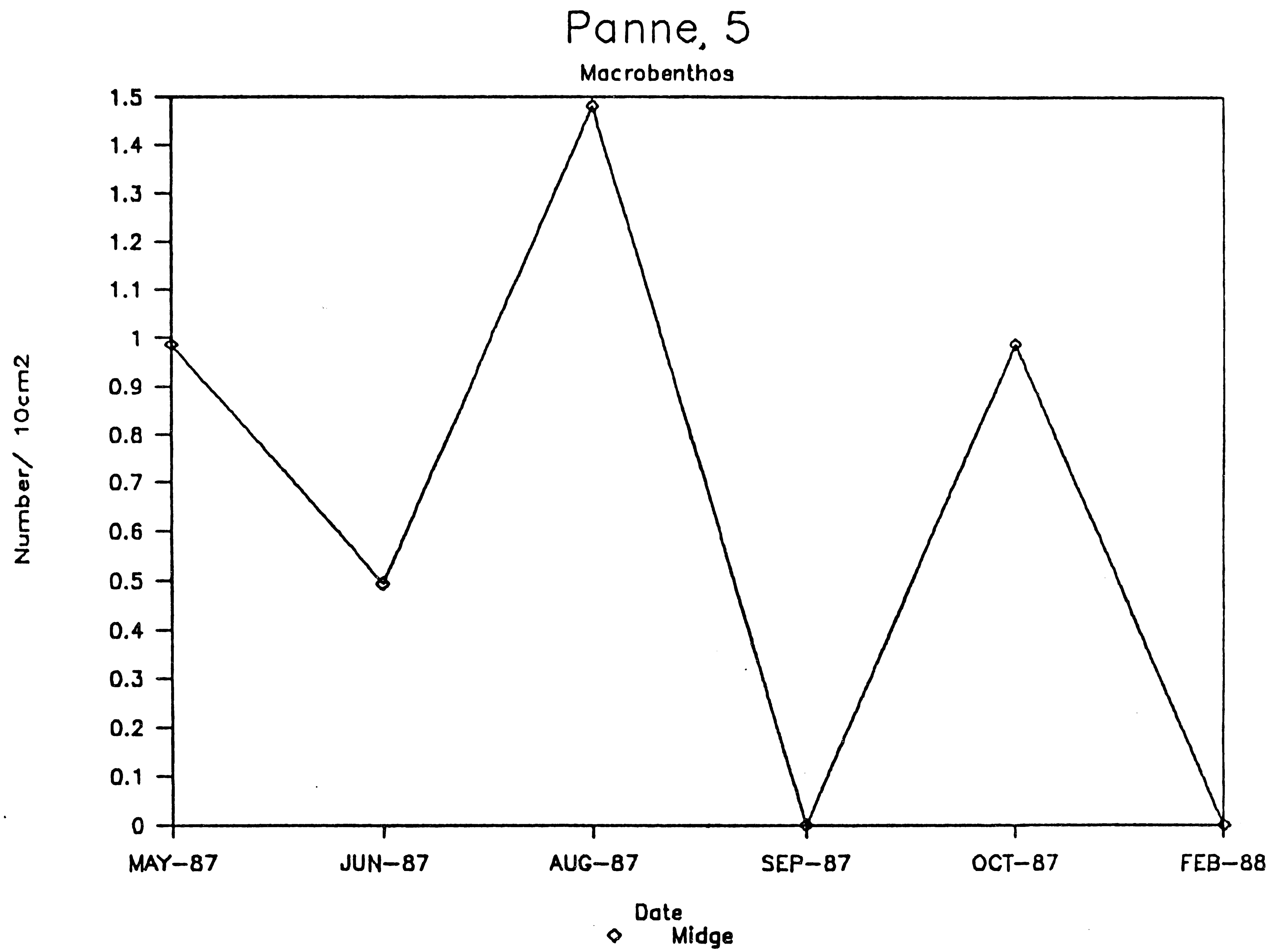
This appendix contains graphs of all the raw data for the study. The first fifteen graphs are the raw macrobenthos density data for the fifteen study pannes. The next fifteen graphs are the raw temperature data for the pannes, and the last fifteen graphs are the raw salinity data for the pannes. The graphs are interpreted by first reading the heading. This indicates which panne the graph applies to, and whether it is a macrobenthos, temperature, or salinity graph. The macrobenthos graphs include all of the densities from that particular panne for the three dominant macrobenthic organisms, on the sampling date in each month. The temperature data were taken at the time of sampling, as were the salinity data. To find a particular datum just turn to the graph for that panne, in the correct section, macrobenthos, temperature, or salinity, and look at the information on the graph for that particular date.

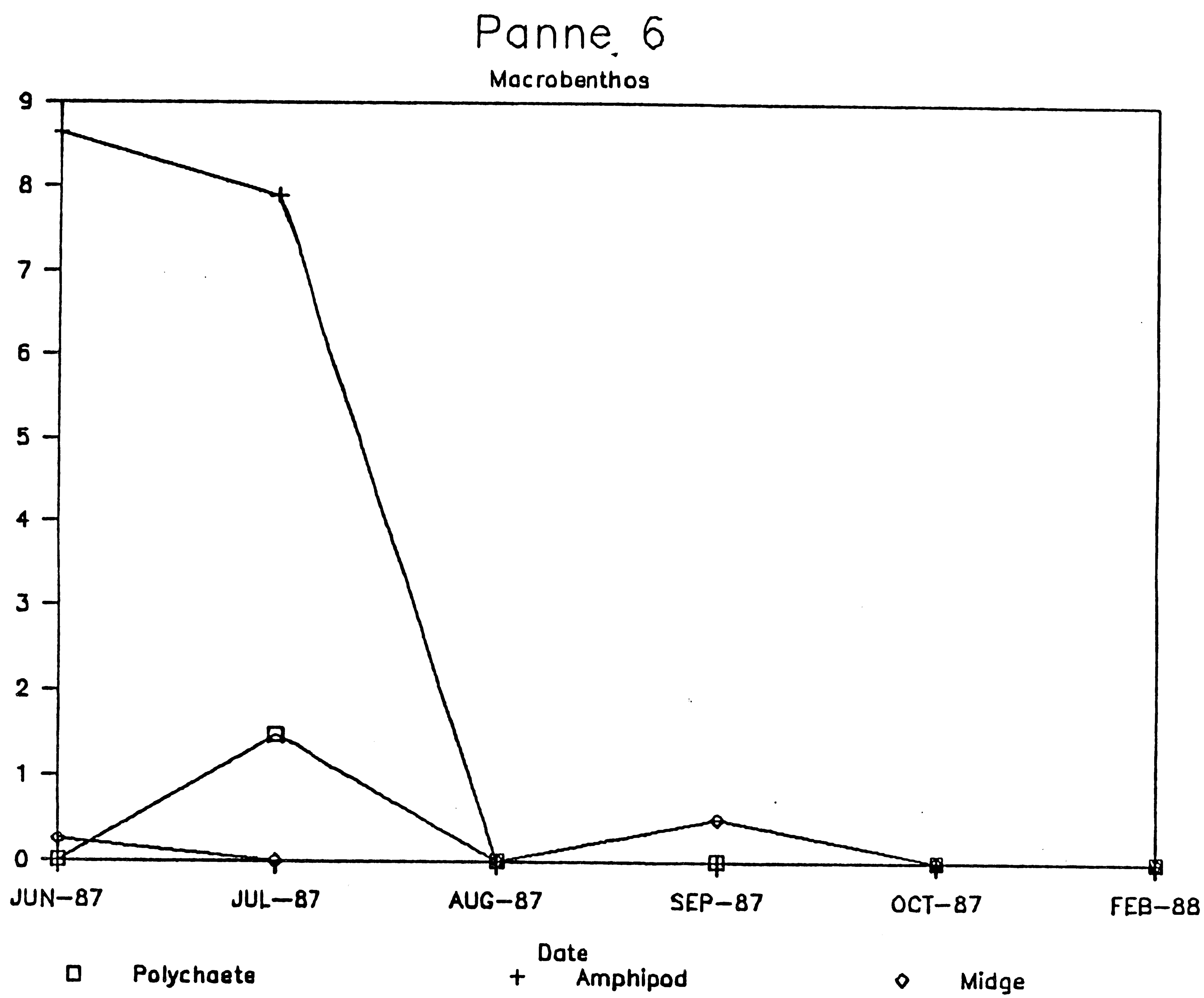

Panne 1
Macrobenthos
20
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
Number/ 10cm2
MAY-87
JUN-87
AUG-87
SEP-87
OCT-87
FEB-88
Date
Polychaete
Amphipod
Midge


Panne 2
Macrobenthos
Number/ 10cm2
0
1
2
3
4
5
6
7
MAY-87
JUN-87
AUG-87
SEP-87
OCT-87
FEB-88
Date
+ Amphipod
◇ Midge

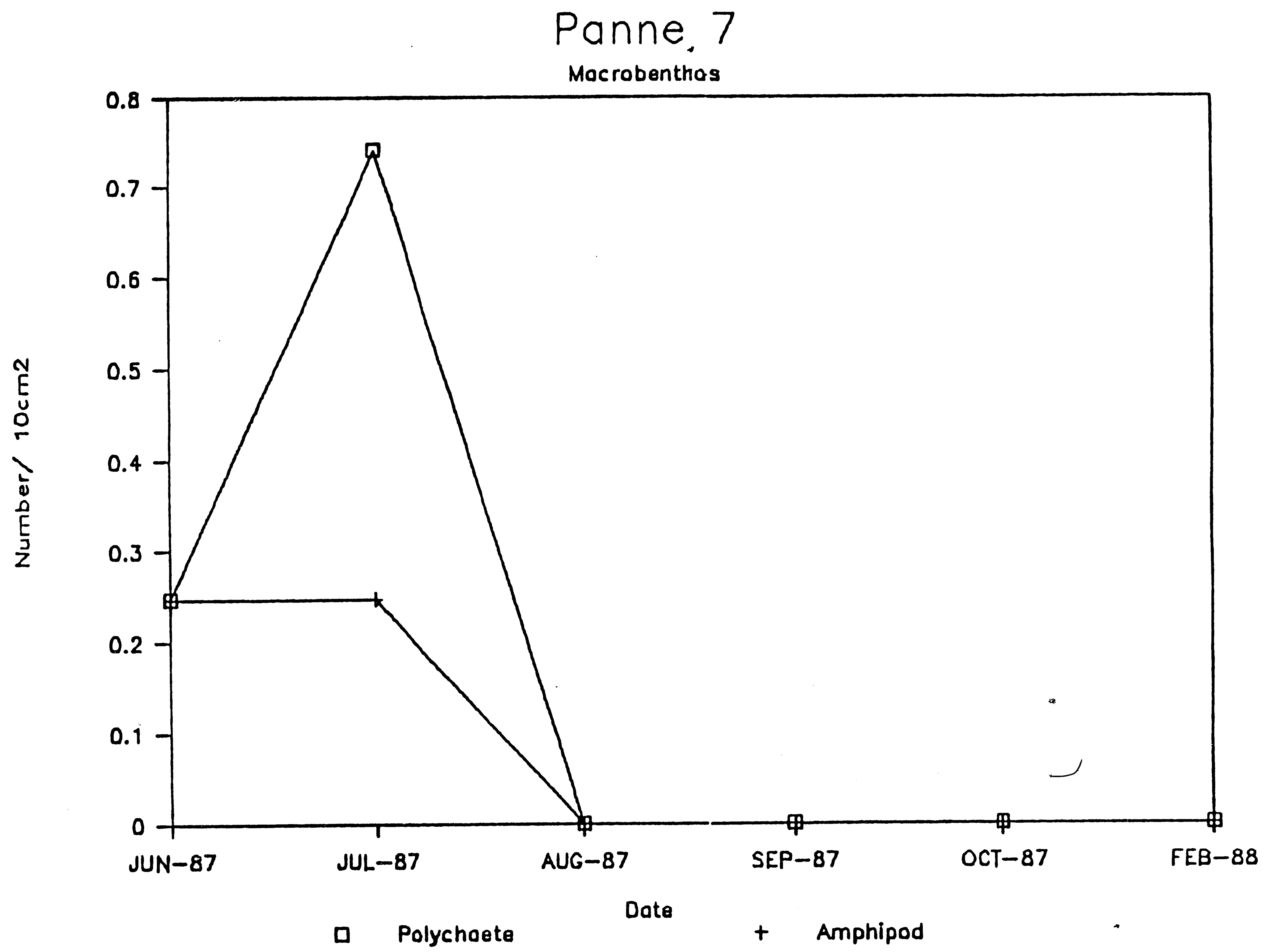

Panne 3
Macrobenthos
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Number/ 10cm2
MAY-87
JUN-87
AUG-87
SEP-87
OCT-87
FEB-88
Date
Polychaete
Amphipod


Panne, 4
Macrobenthos
Number/ 10cm2
34
32
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
MAY-87
JUN-87
AUG-87
SEP-87
OCT-87
FEB-88
Date
Polychaete
Amphipod
Midge


Panne, 5
Macrobenthos
Number/ 10cm2
1.5
1.4
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
MAY-87
JUN-87
AUG-87
SEP-87
OCT-87
FEB-88
Date
Midge



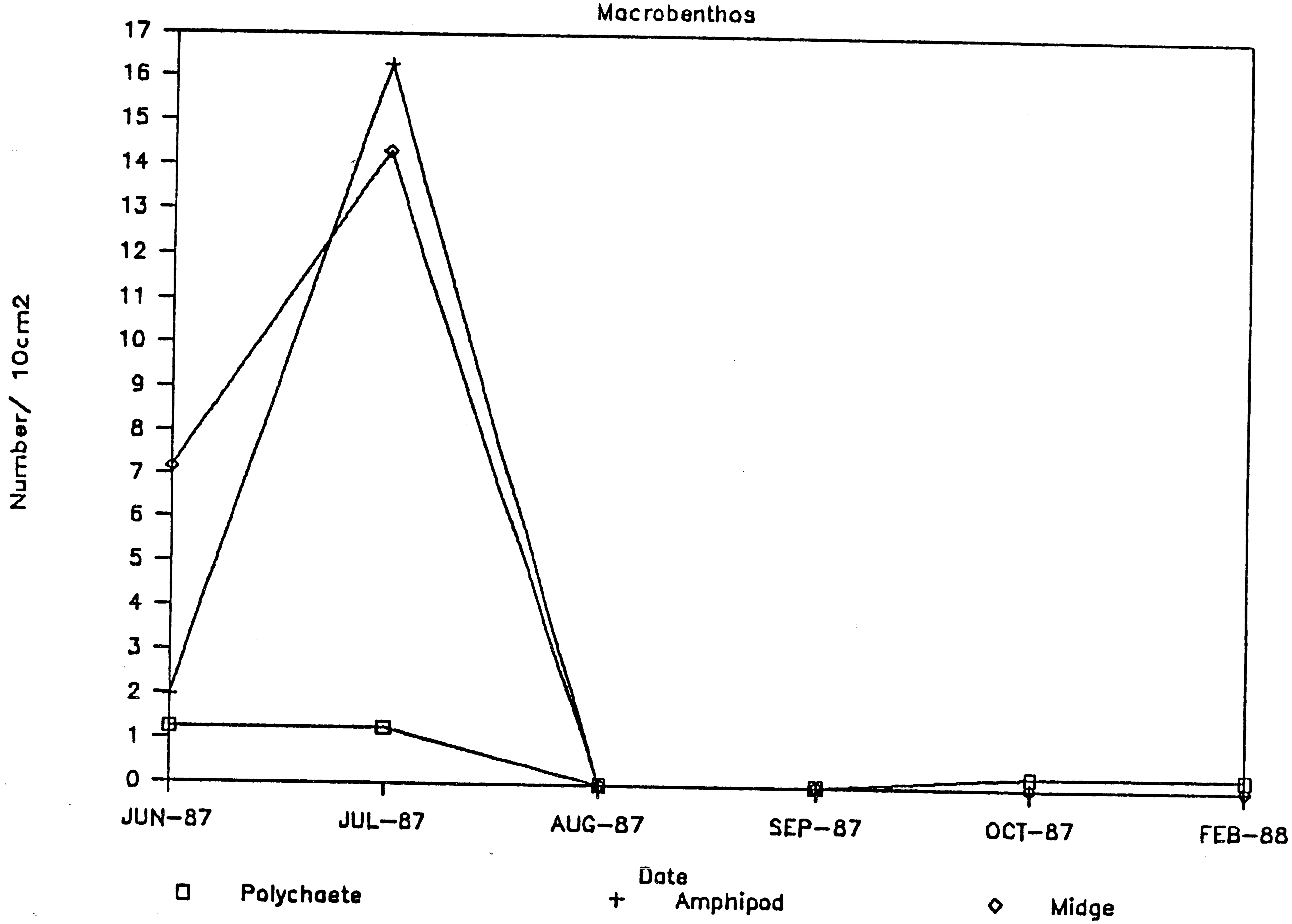
Panne 6
Macrobenthos
Number/ 10cm2
9
8
7
6
5
4
3
2
1
0
JUN-87
JUL-87
AUG-87
SEP-87
OCT-87
FEB-88
Date
Polychaete
Amphipod
Midge

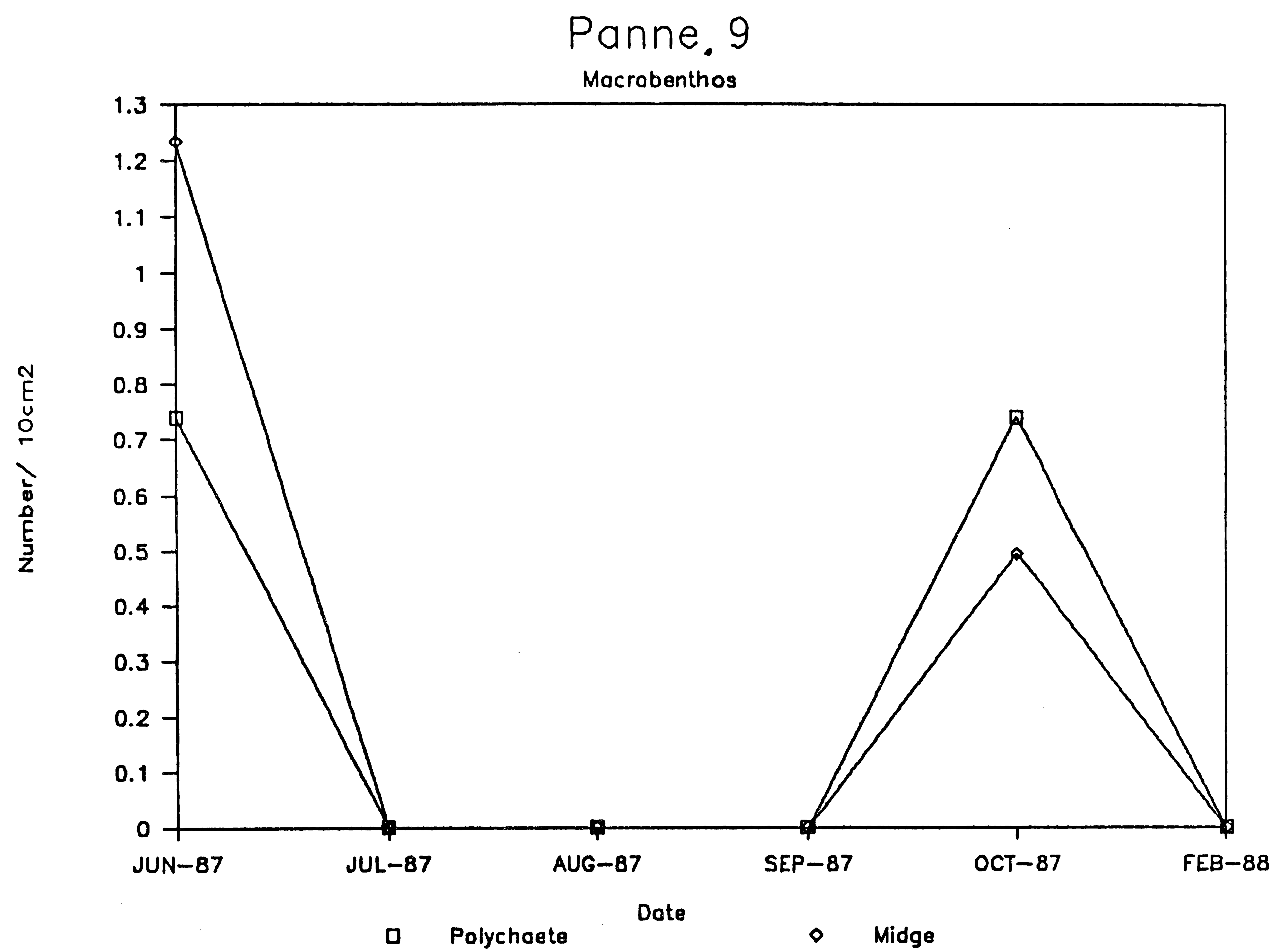


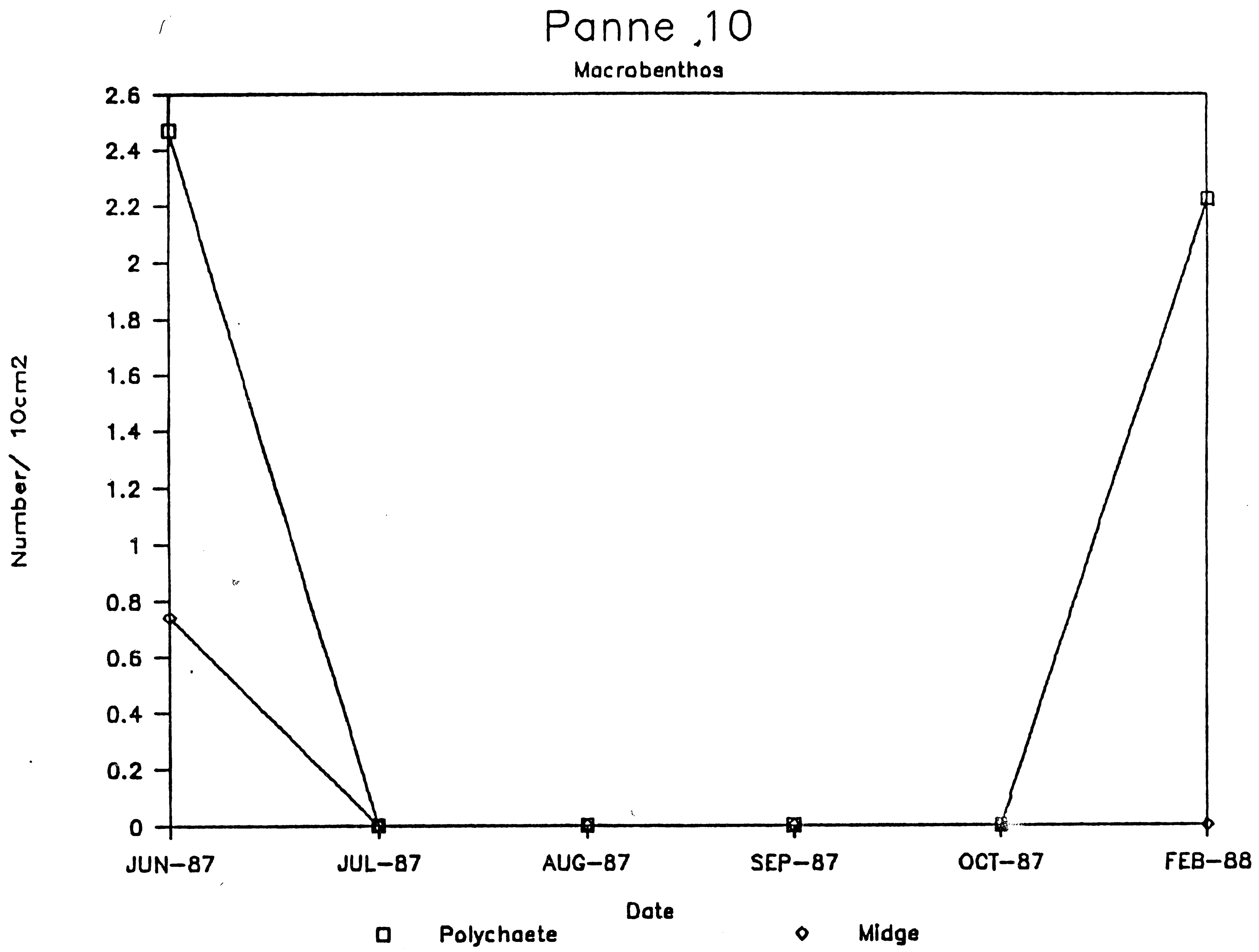
Panne 7
Macrobenthos
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Number/ 10cm2
JUN-87
JUL-87
AUG-87
SEP-87
OCT-87
FEB-88
Date
Polychaete
Amphipod

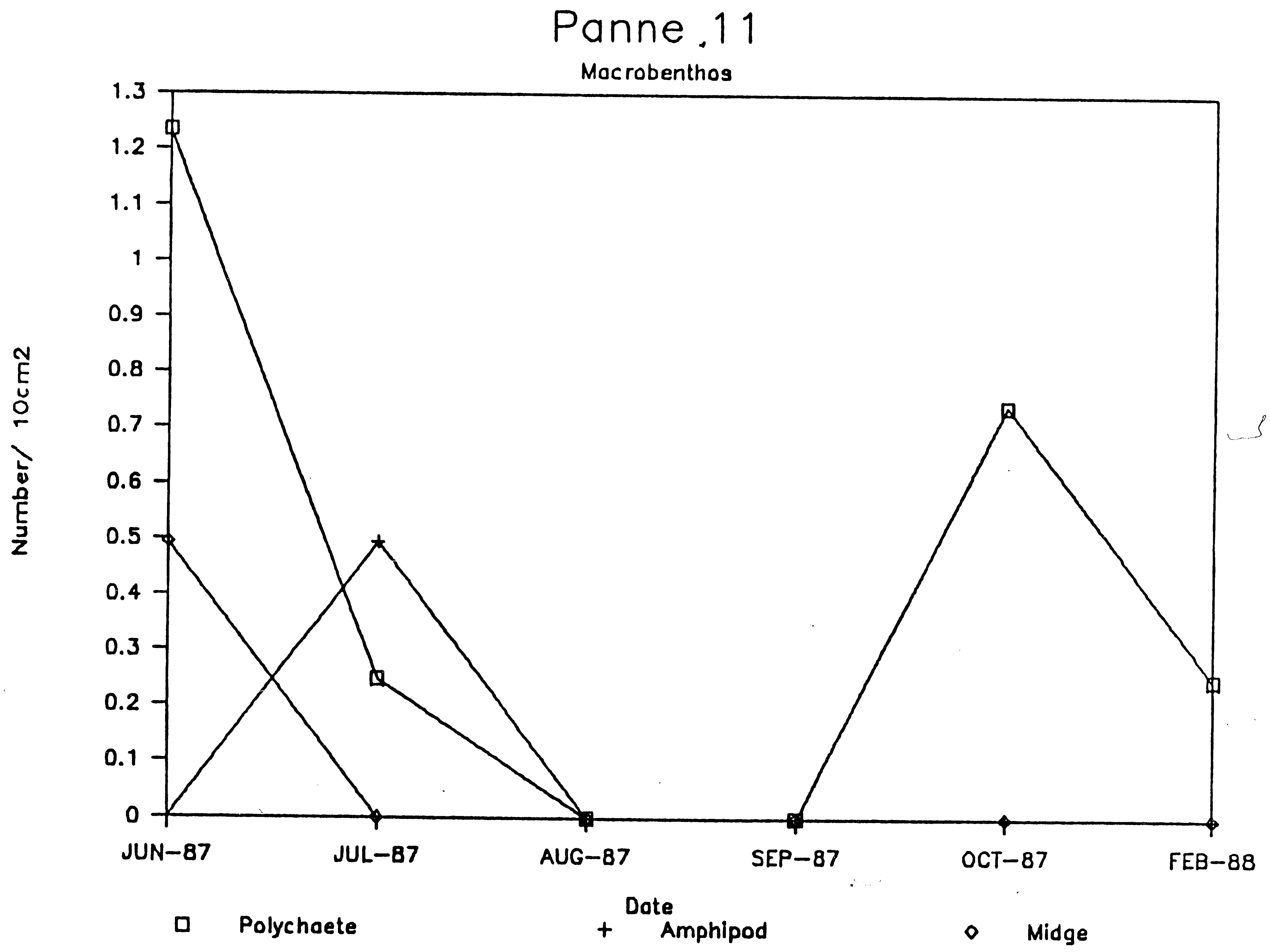
Panne 8

Macrobenthos

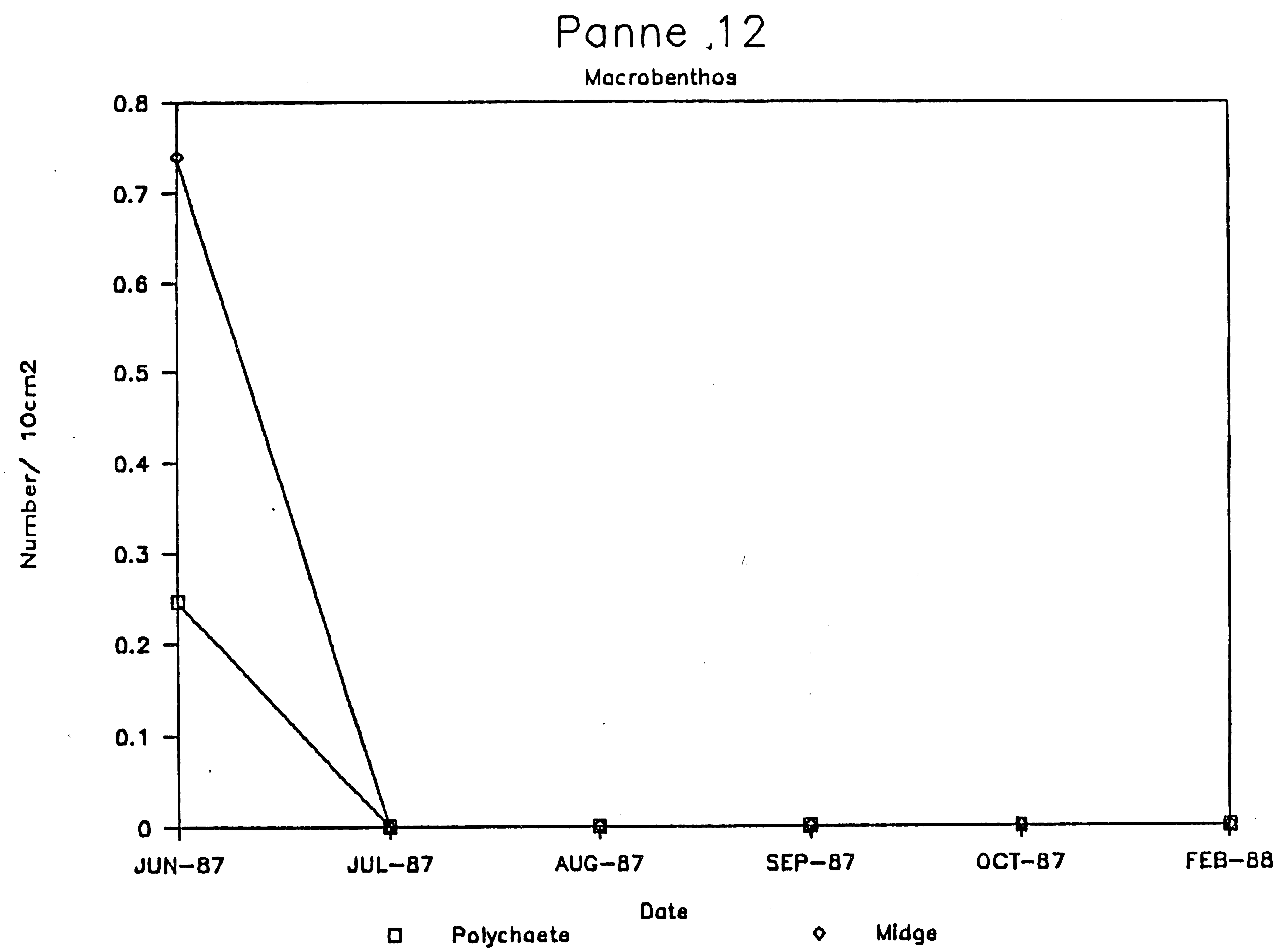



Panne, 9
Macrobenthos
Number/ 10cm2
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
JUN-87
JUL-87
AUG-87
SEP-87
OCT-87
FEB-88
Date
Polychaete
Midge


Panne 10
Macrobenthos
Number/ 10cm2
2.6
2.4
2.2
2
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
JUN-87
JUL-87
AUG-87
SEP-87
OCT-87
FEB-88
Date
Polychaete
Midge



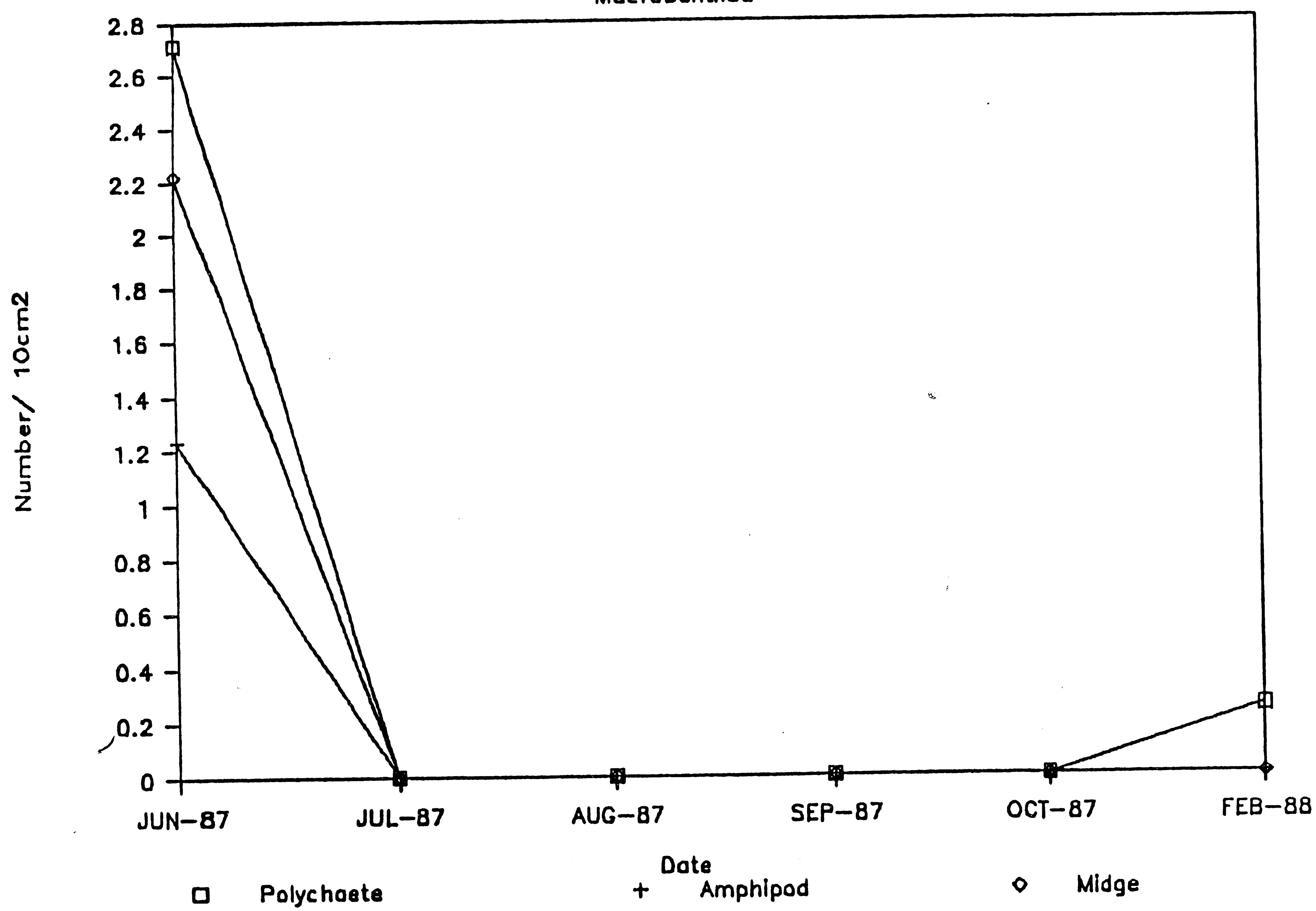
Panne 11
Macrobenthos
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Number/ 10cm2
JUN-87
JUL-87
AUG-87
SEP-87
OCT-87
FEB-88
Date
Polychaete
Amphipod
Midge

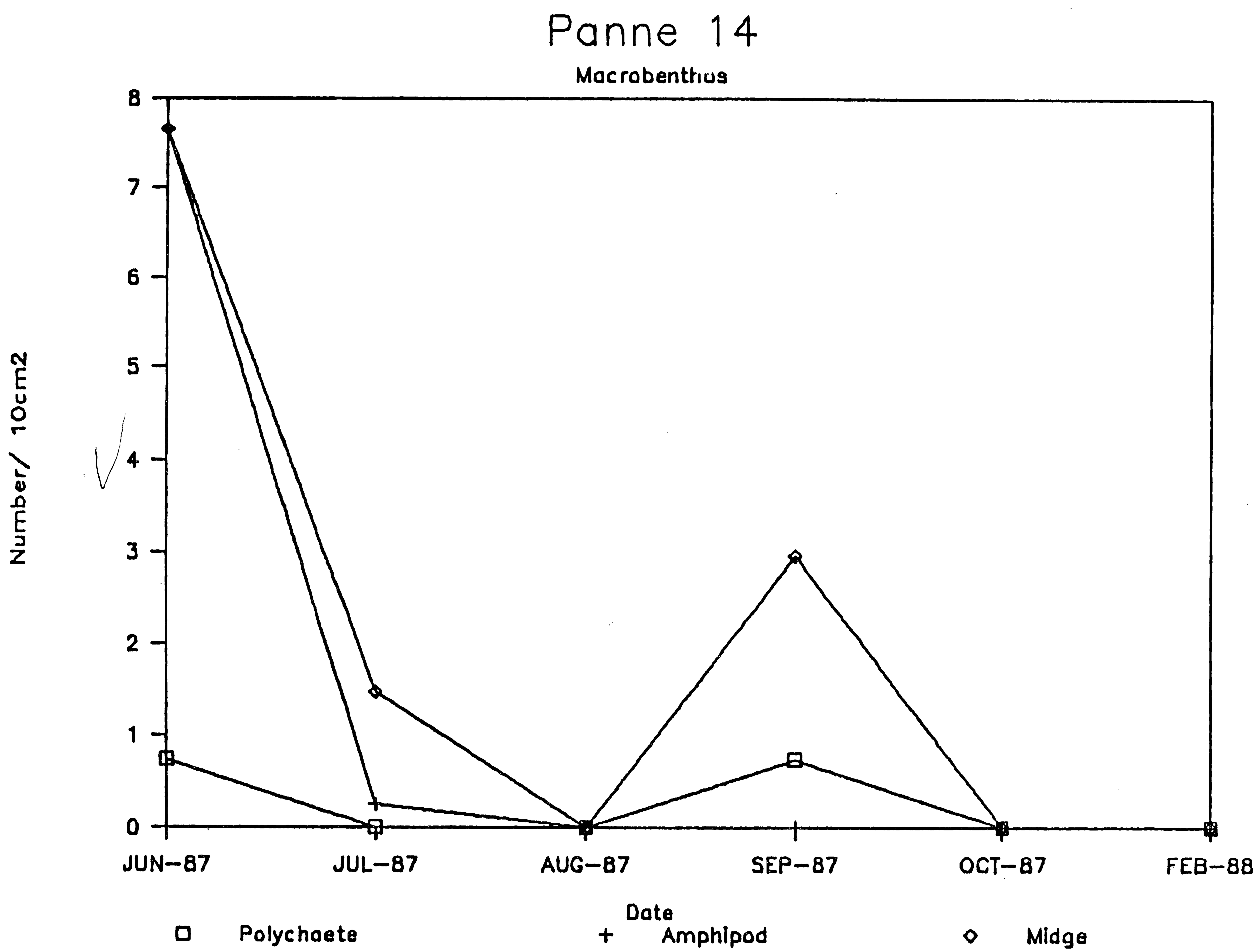


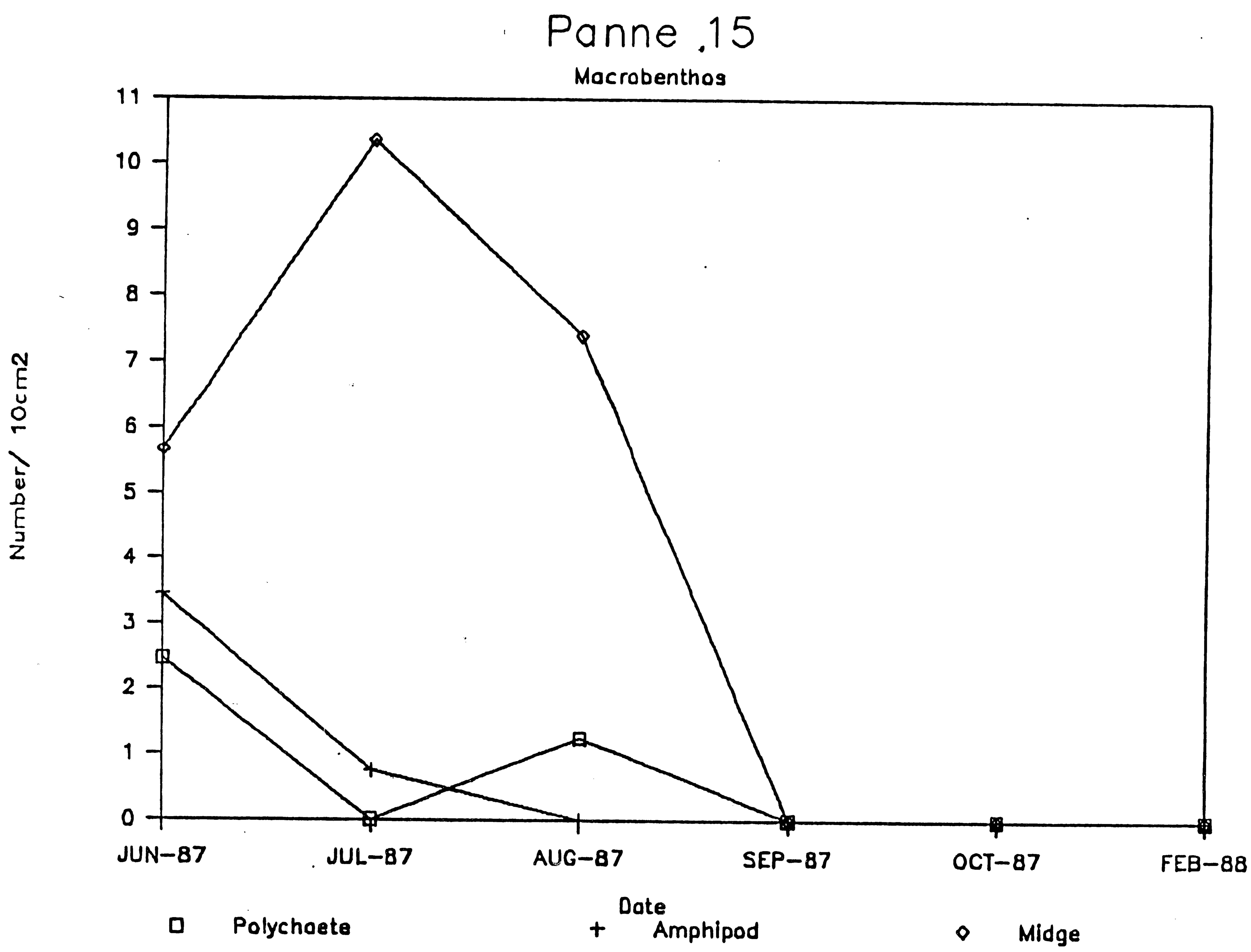
Panne .12
Macrobenthos
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Number/ 10cm2
JUN-87
JUL-87
AUG-87
SEP-87
OCT-87
FEB-88
Date
Polychaete
Midge

Panne 13

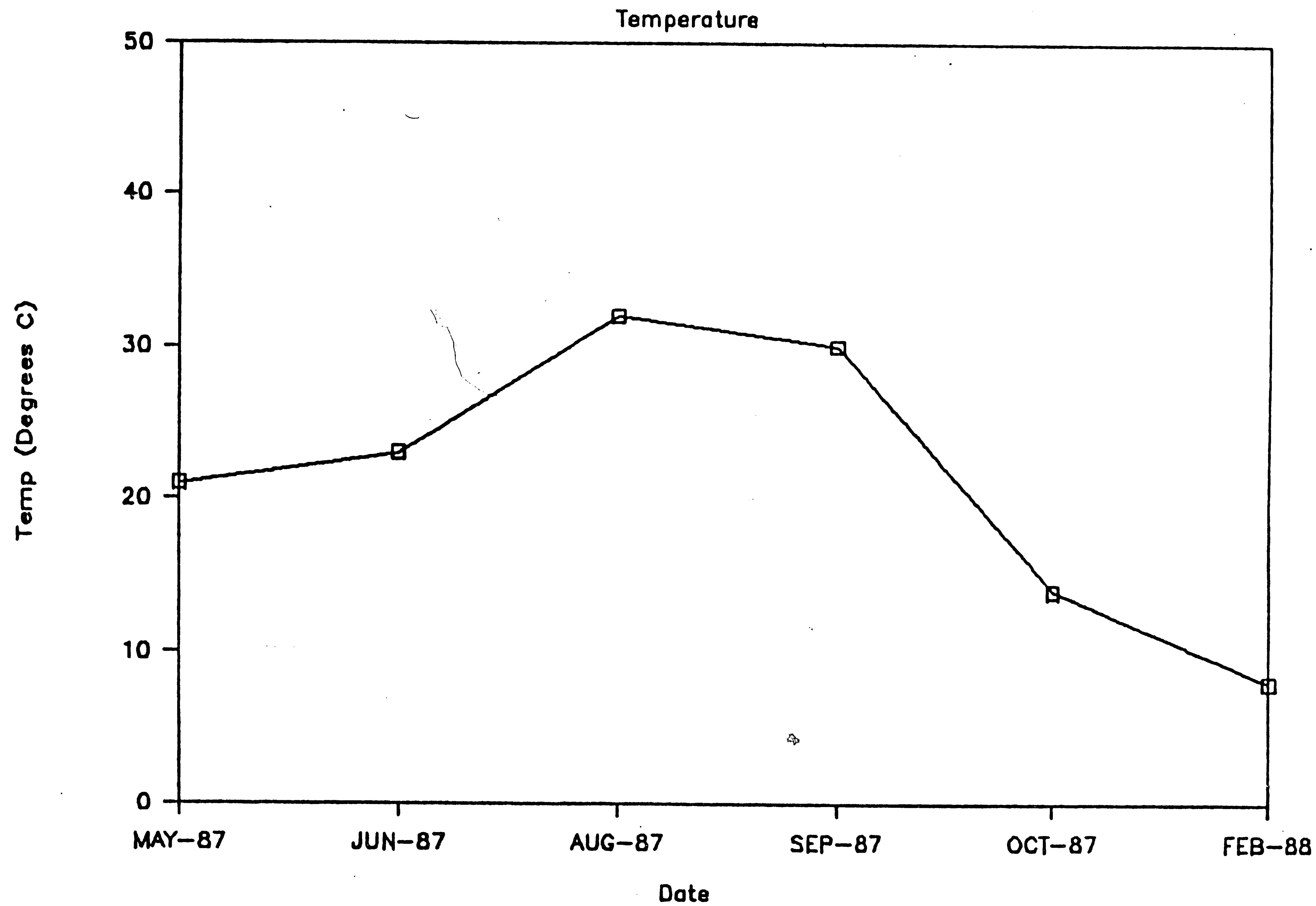
Macrobenthos




Panne 14
Macrobenthos
Number/ 10cm2
8
7
6
5
4
3
2
1
0
JUN-87
JUL-87
AUG-87
SEP-87
OCT-87
FEB-88
Date
Polychaete
Amphipod
Midge


Panne .15
Macrobenthos
Number/ 10cm2
11
10
9
8
7
6
5
4
3
2
1
0
JUN-87
JUL-87
AUG-87
SEP-87
OCT-87
FEB-88
Date
Polychaete
Amphipod
Midge

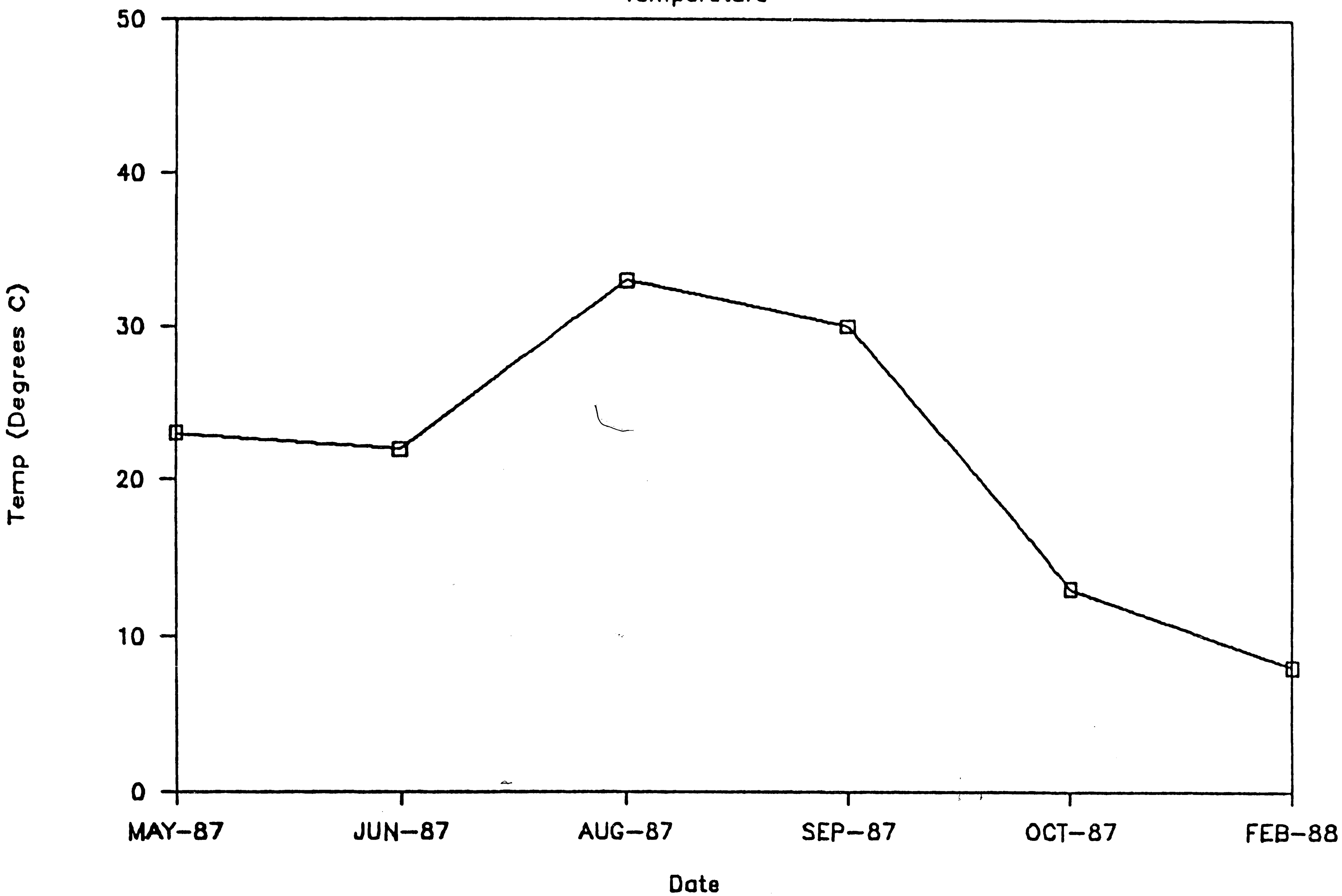
Panne 1

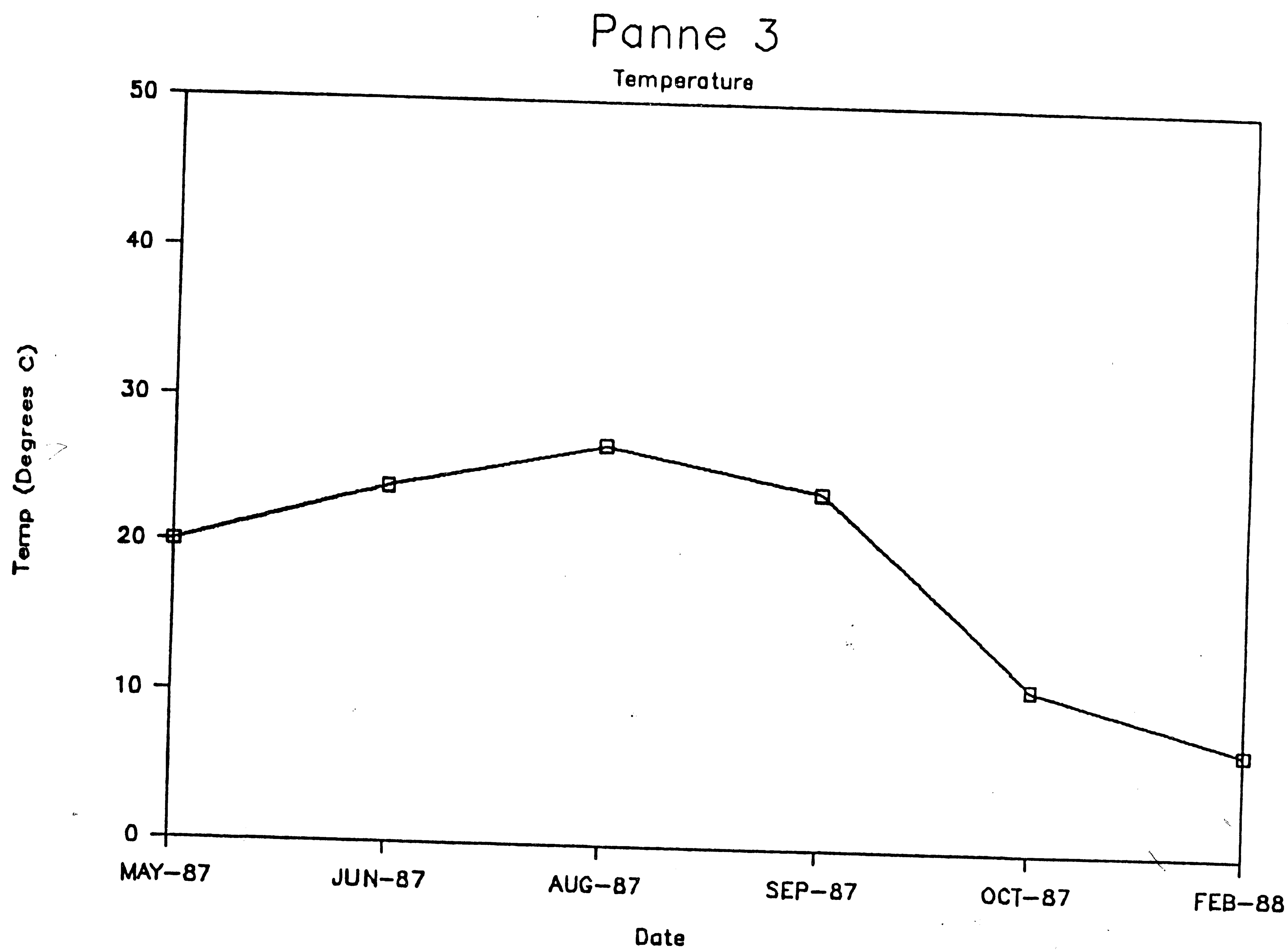


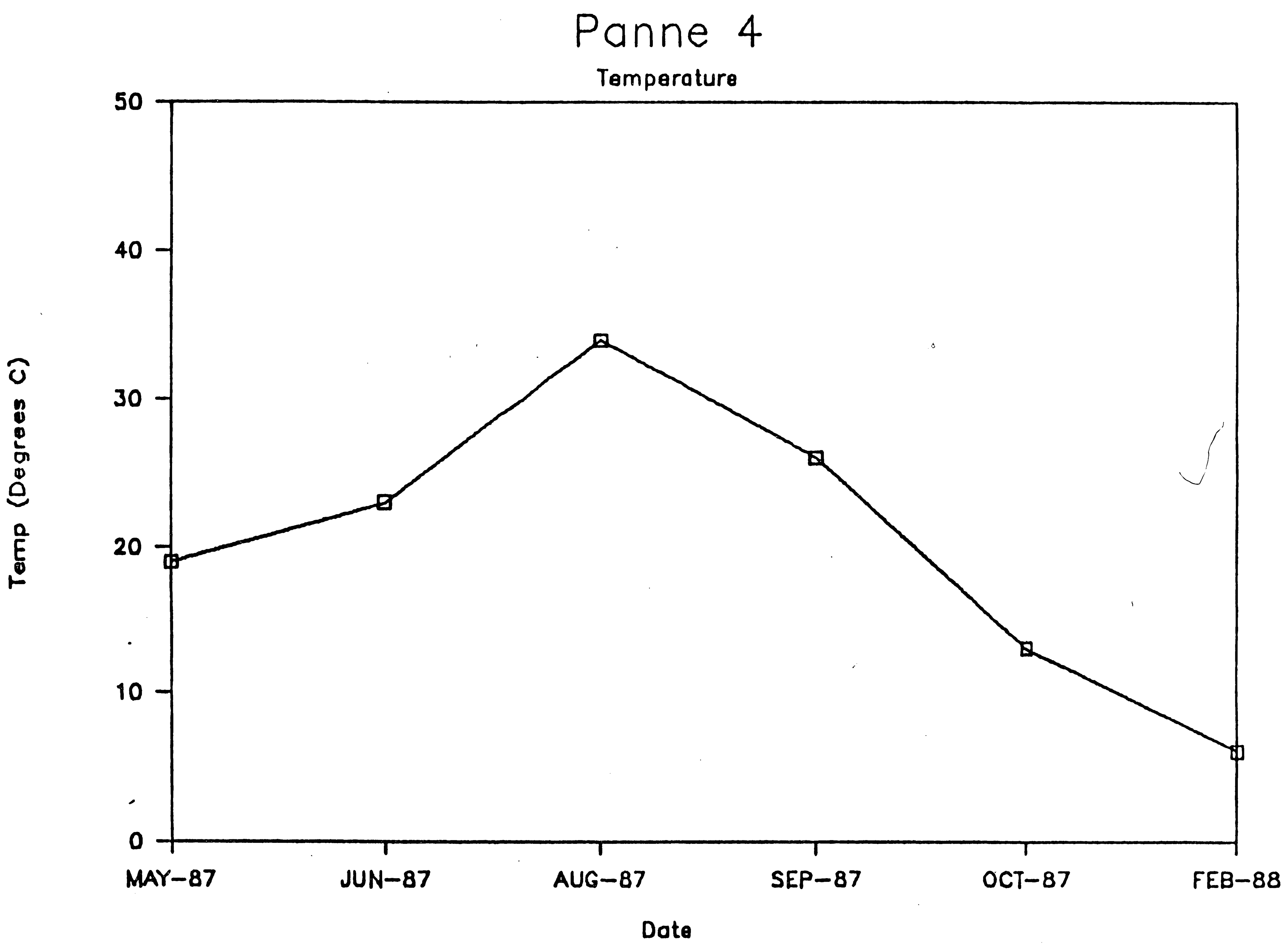
Temperature
Temp (Degrees C)
0
10
20
30
40
50
MAY-87
JUN-87
AUG-87
SEP-87
OCT-87
FEB-88
Date

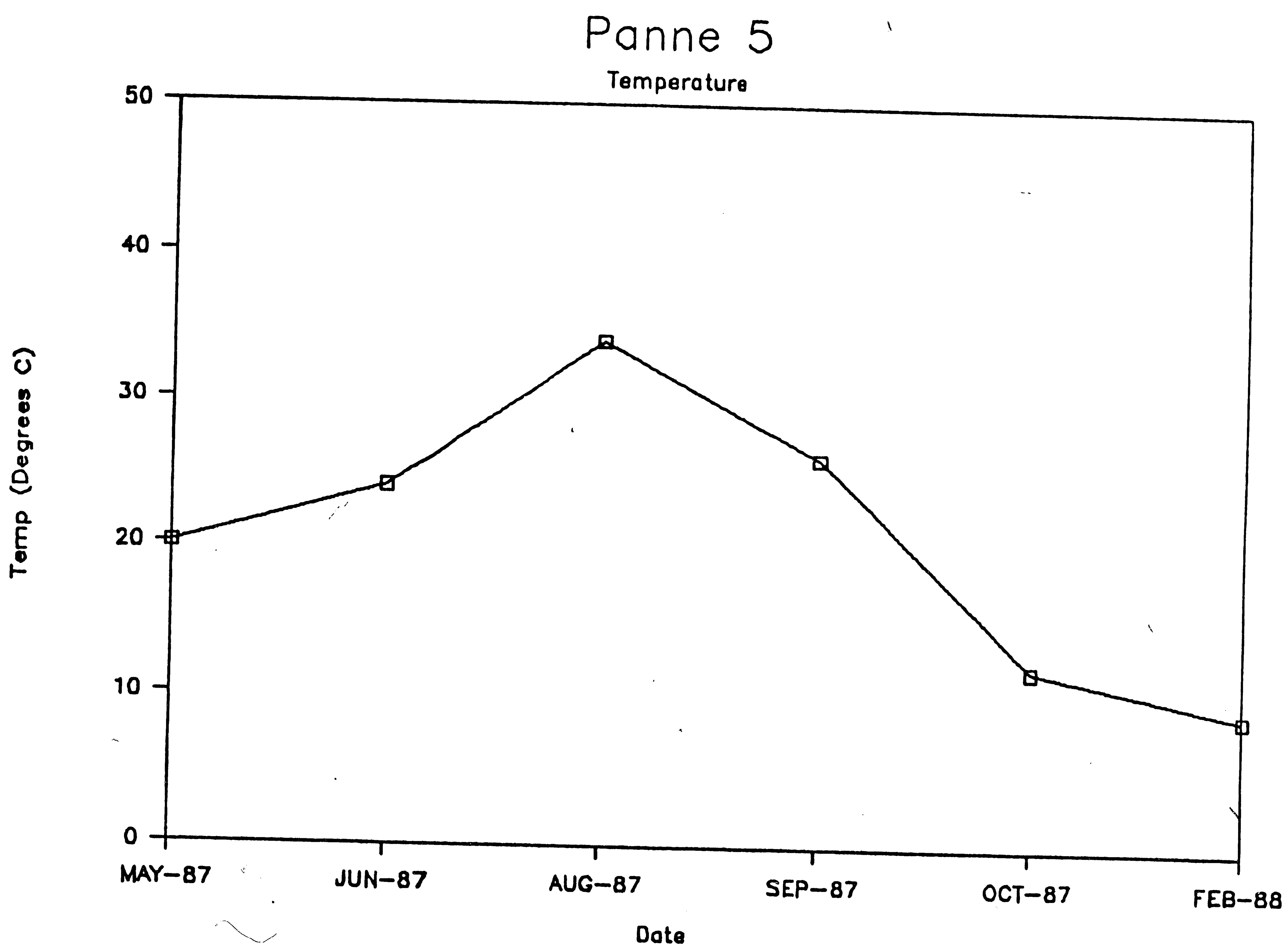
Panne 2

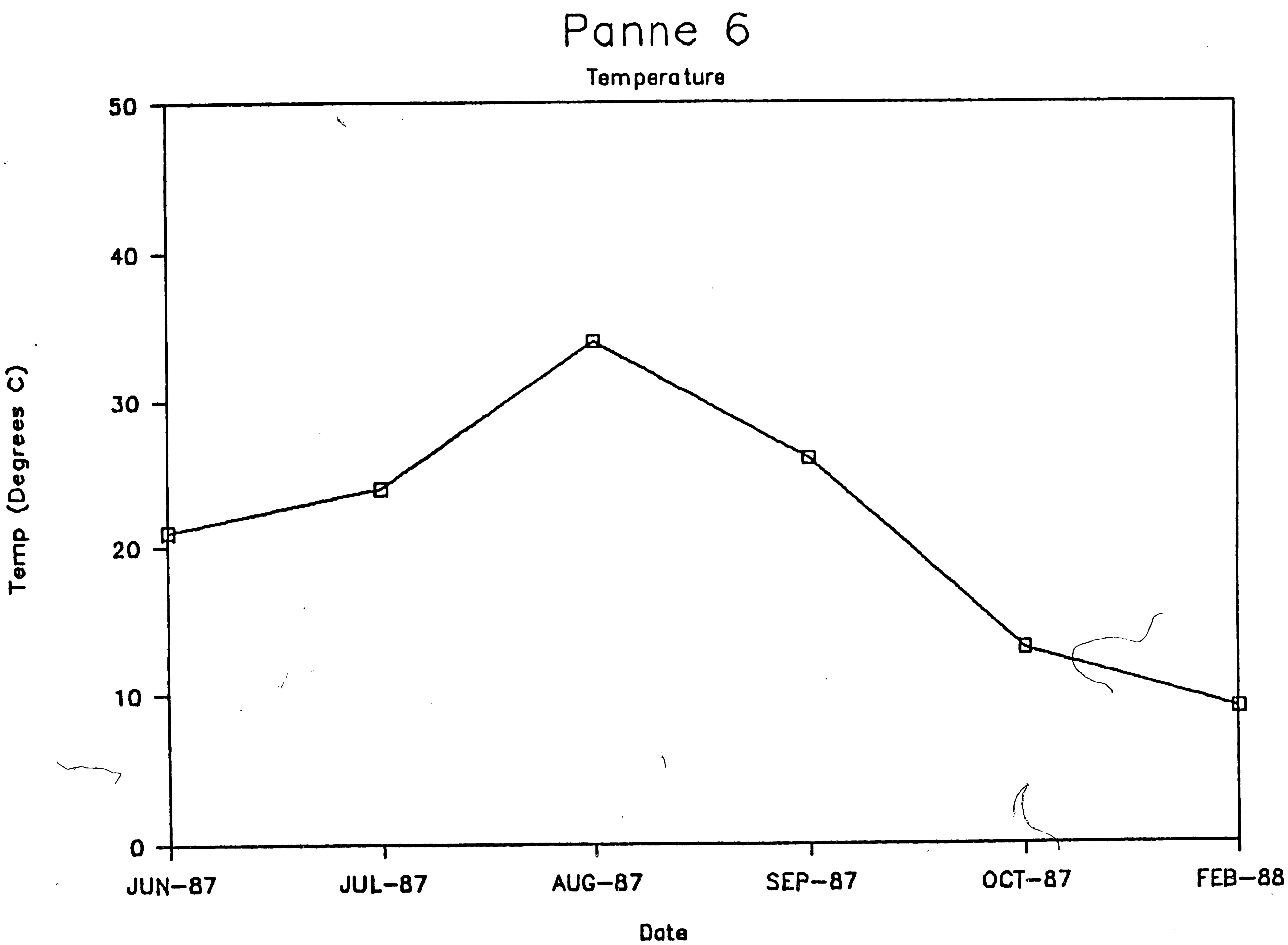
Temperature




Panne 3
Temperature
Temp (Degrees C)
50
40
30
20
10
0
MAY–87
JUN–87
AUG–87
SEP–87
OCT–87
FEB–88
Date

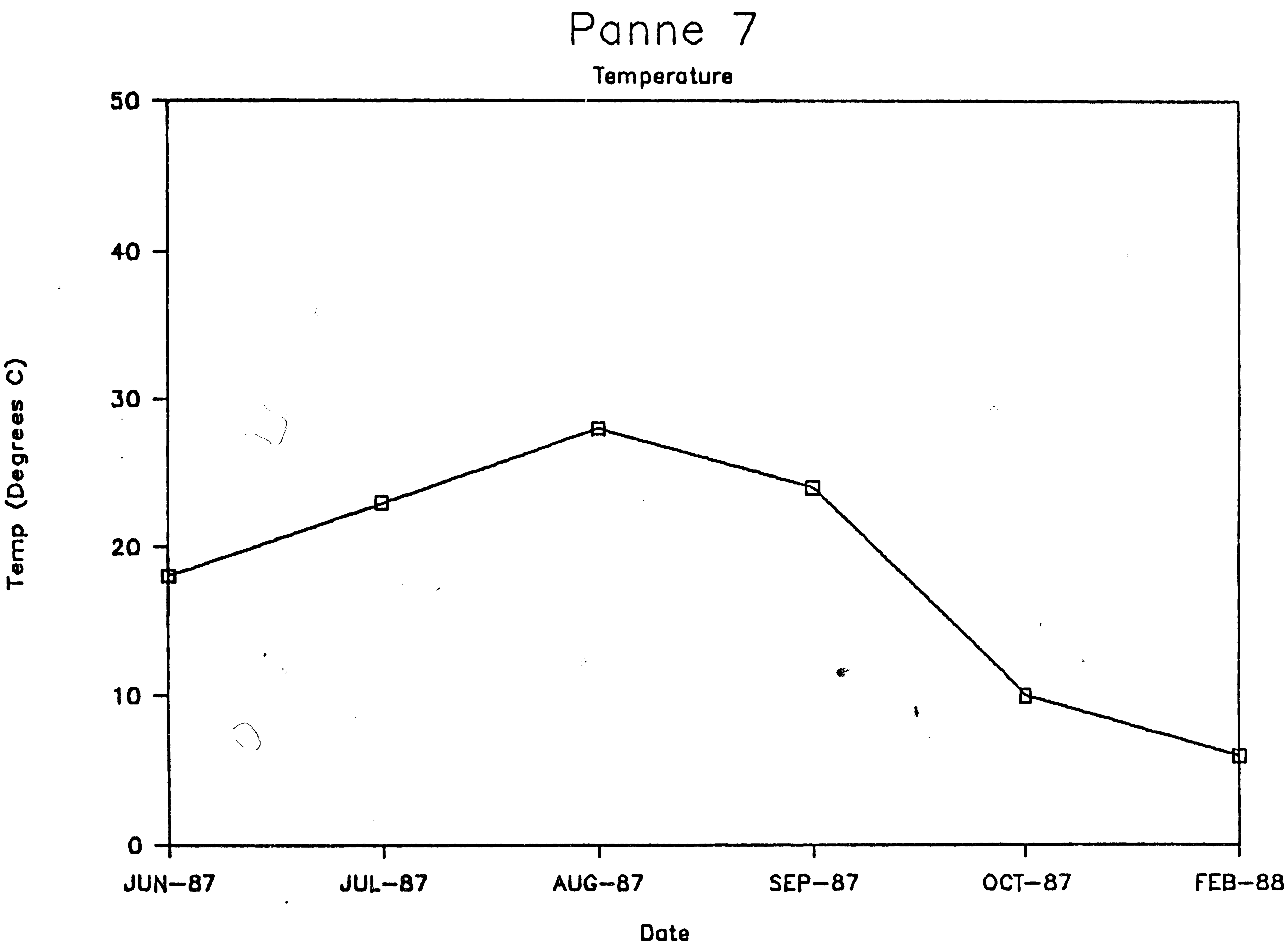

Panne 4
Temperature
Temp (Degrees C)
0
10
20
30
40
50
MAY-87
JUN-87
AUG-87
SEP-87
OCT-87
FEB-88
Date


Panne 5
Temperature
Temp (Degrees C)
50
40
30
20
10
0
MAY-87
JUN-87
AUG-87
SEP-87
OCT-87
FEB-88
Date

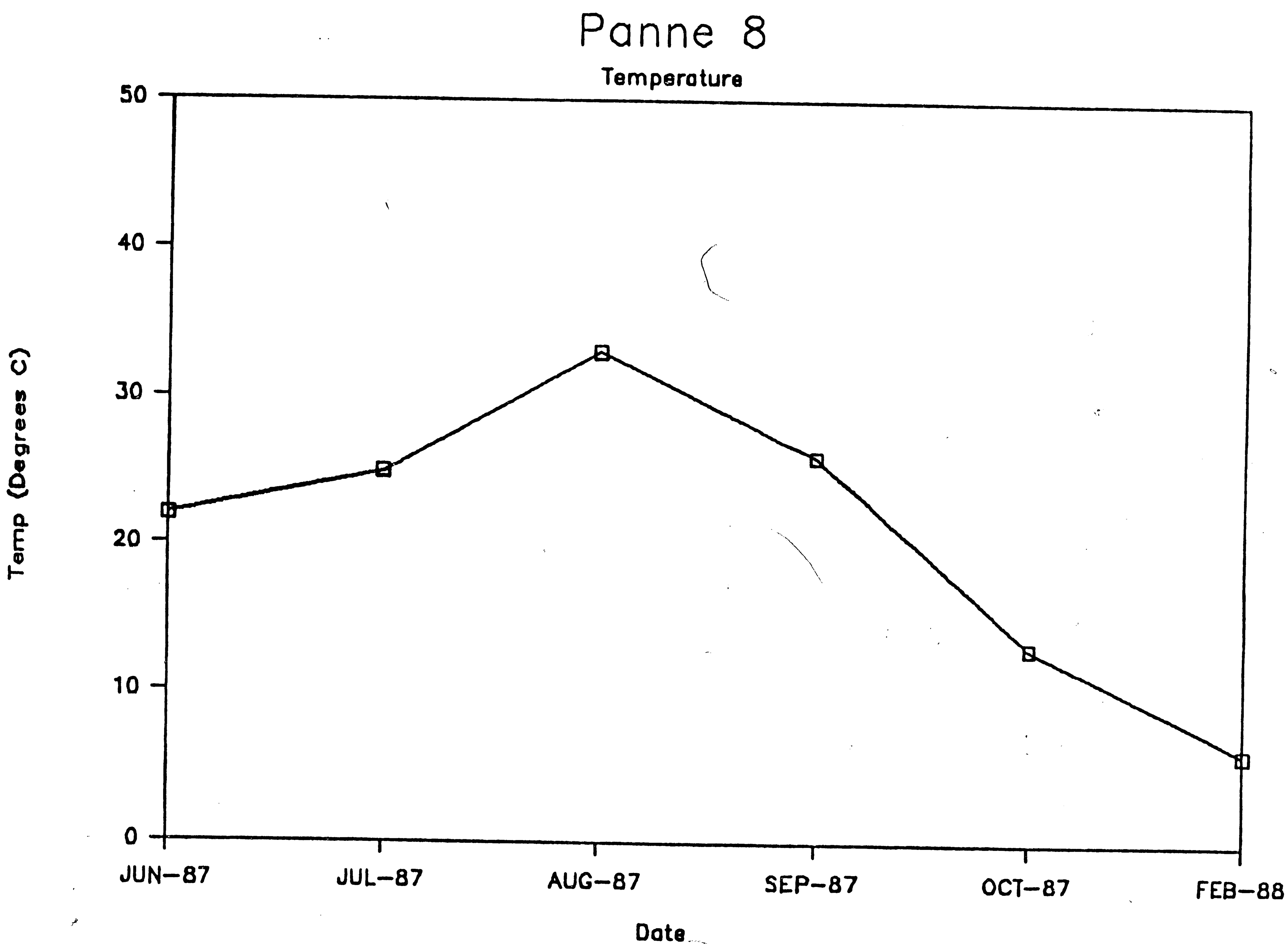


Panne 6
Temperature
50
40
30
20
10
0
Temp (Degrees C)
JUN-87
JUL-87
AUG-87
SEP-87
OCT-87
FEB-88
Date

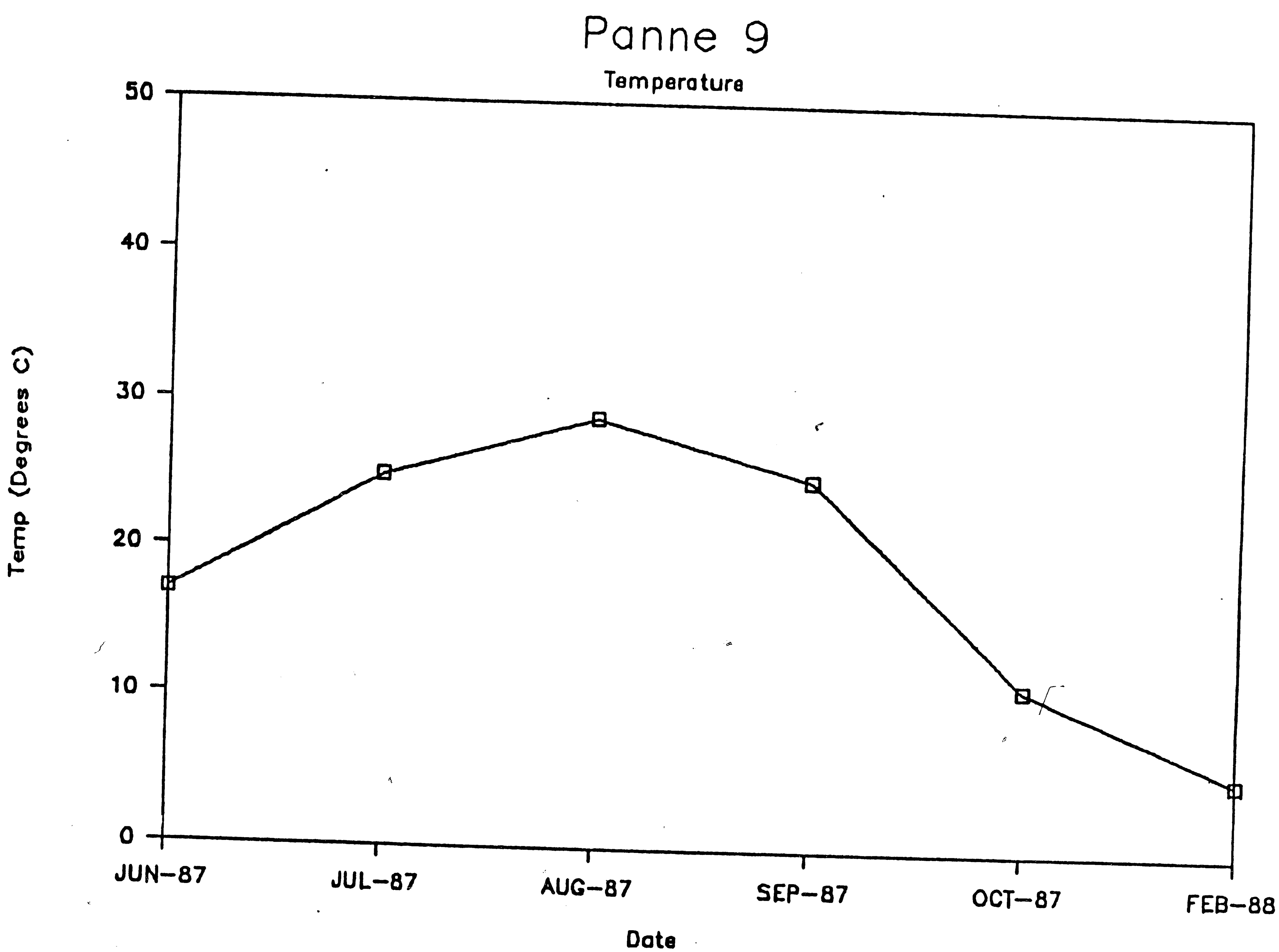
94



Panne 7
Temperature
50
40
30
20
10
0
Temp (Degrees C)
JUN-87
JUL-87
AUG-87
SEP-87
OCT-87
FEB-88
Date

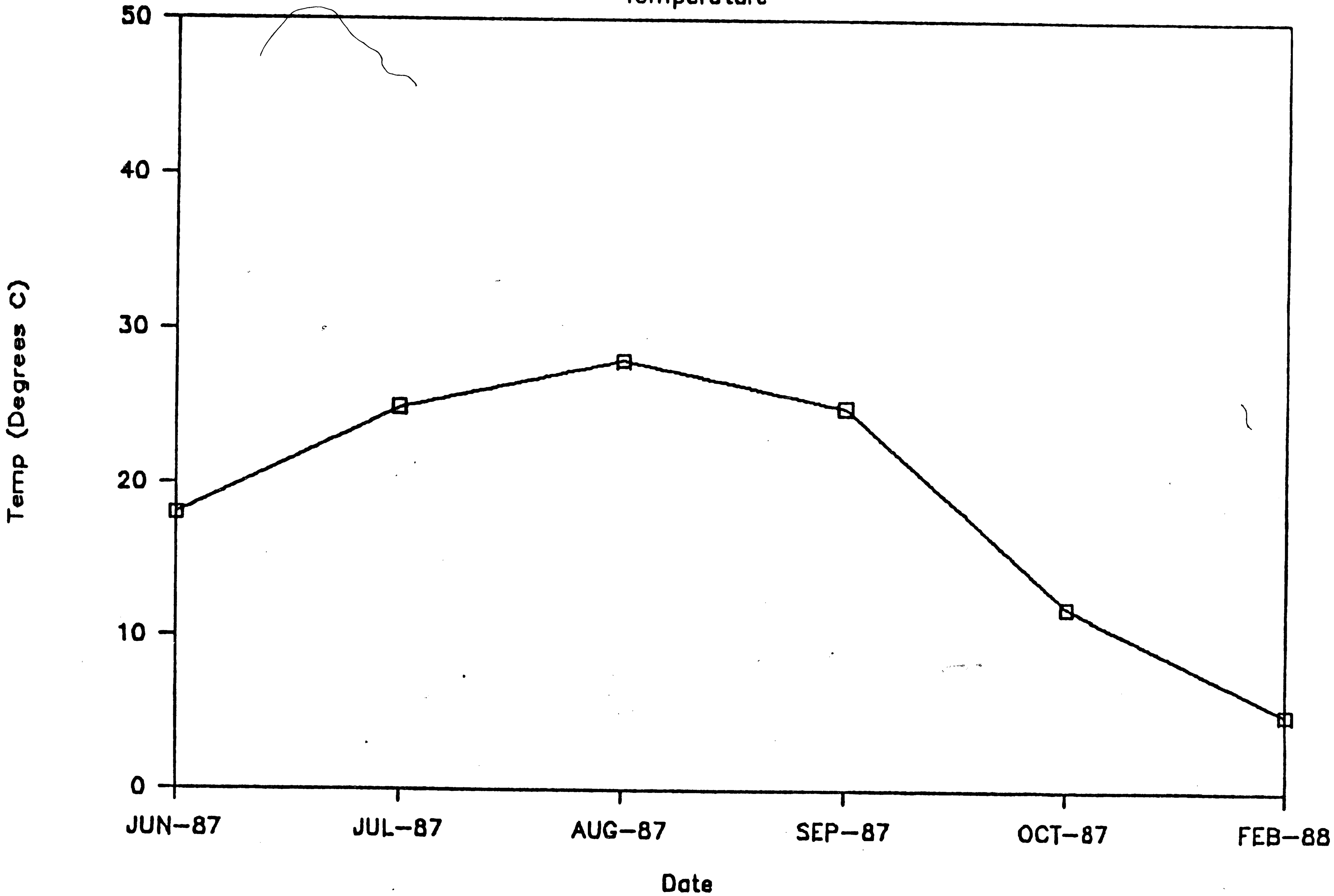


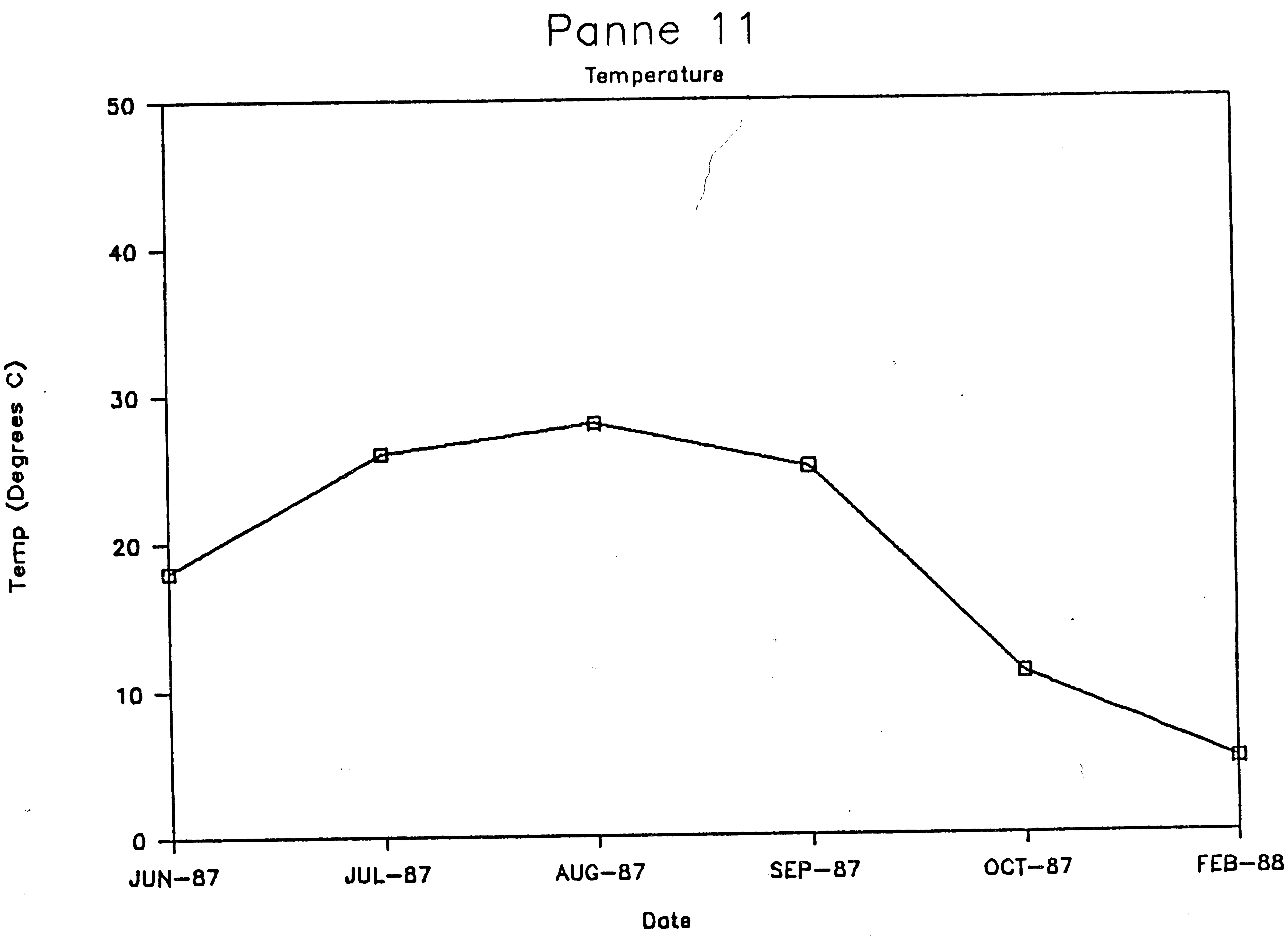
Panne 8
Temperature
Temp (Degrees C)
50
40
30
20
10
0
JUN-87
JUL-87
AUG-87
SEP-87
OCT-87
FEB-88
Date


Panne 9
Temperature
Temp (Degrees C)
50
40
30
20
10
0
JUN-87
JUL-87
AUG-87
SEP-87
OCT-87
FEB-88
Date

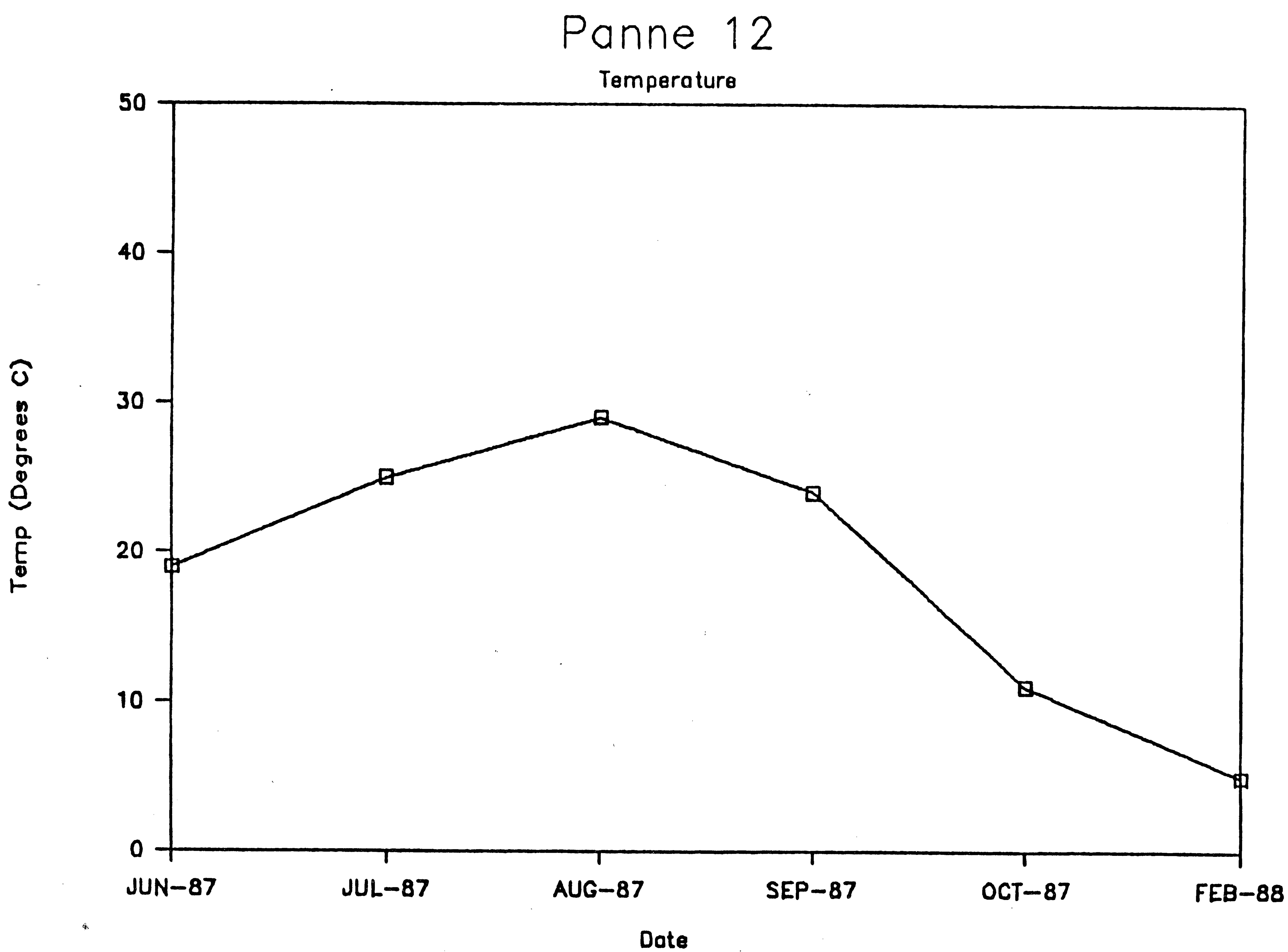
Panne 10

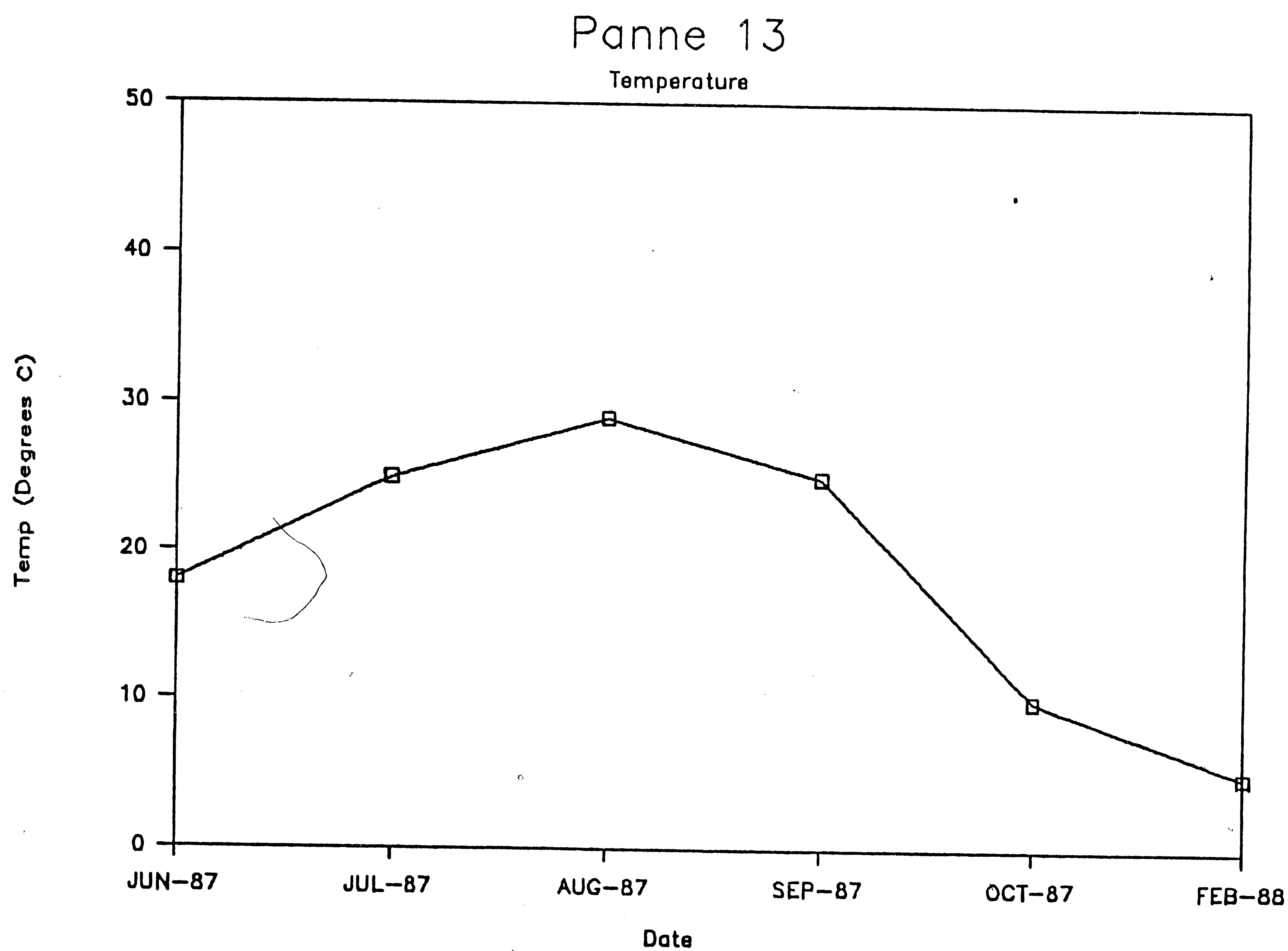
Temperature





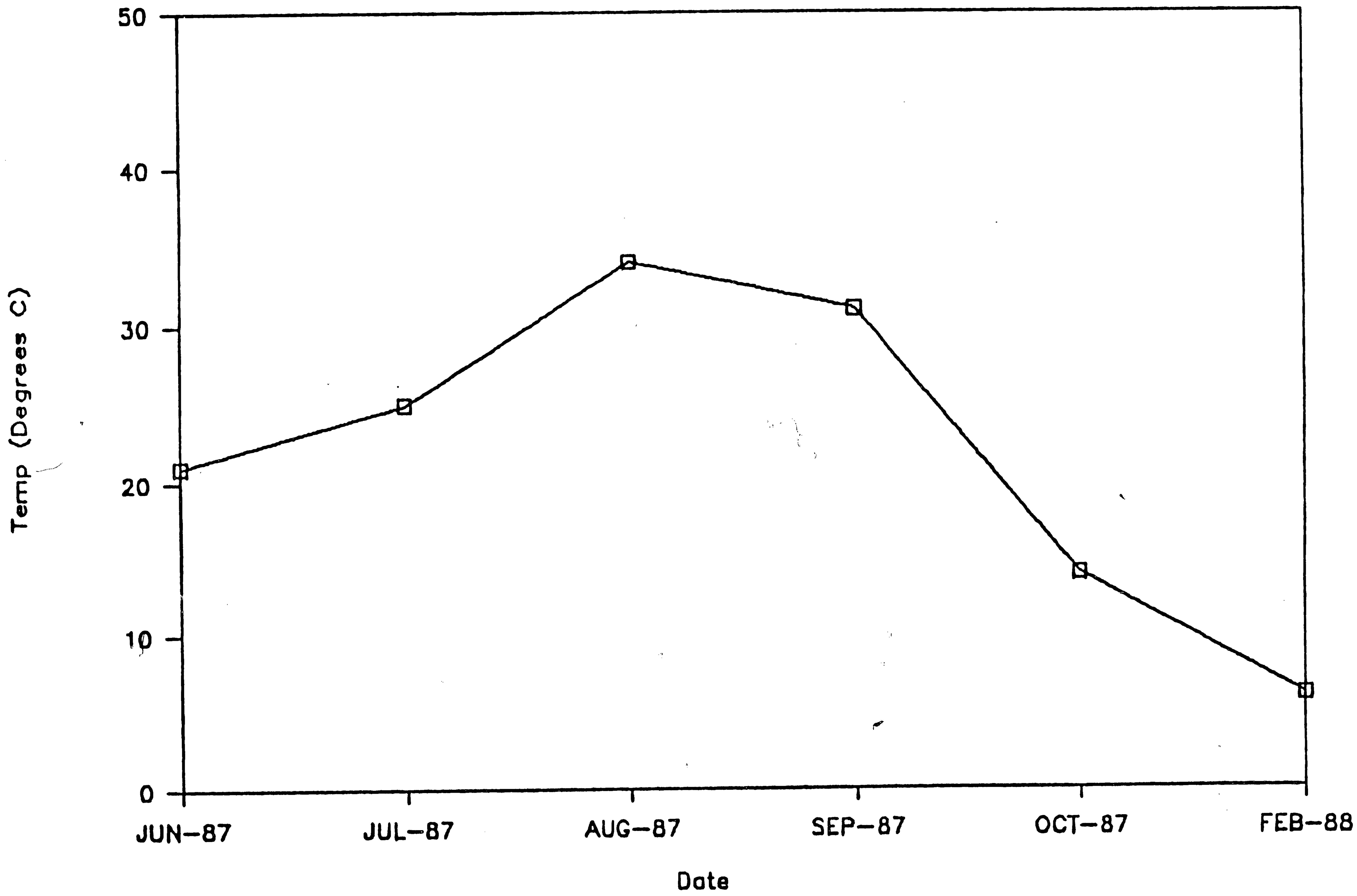
Panne 11
Temperature
Temp (Degrees C)
0
10
20
30
40
50
JUN-87
JUL-87
AUG-87
SEP-87
OCT-87
FEB-88
Date

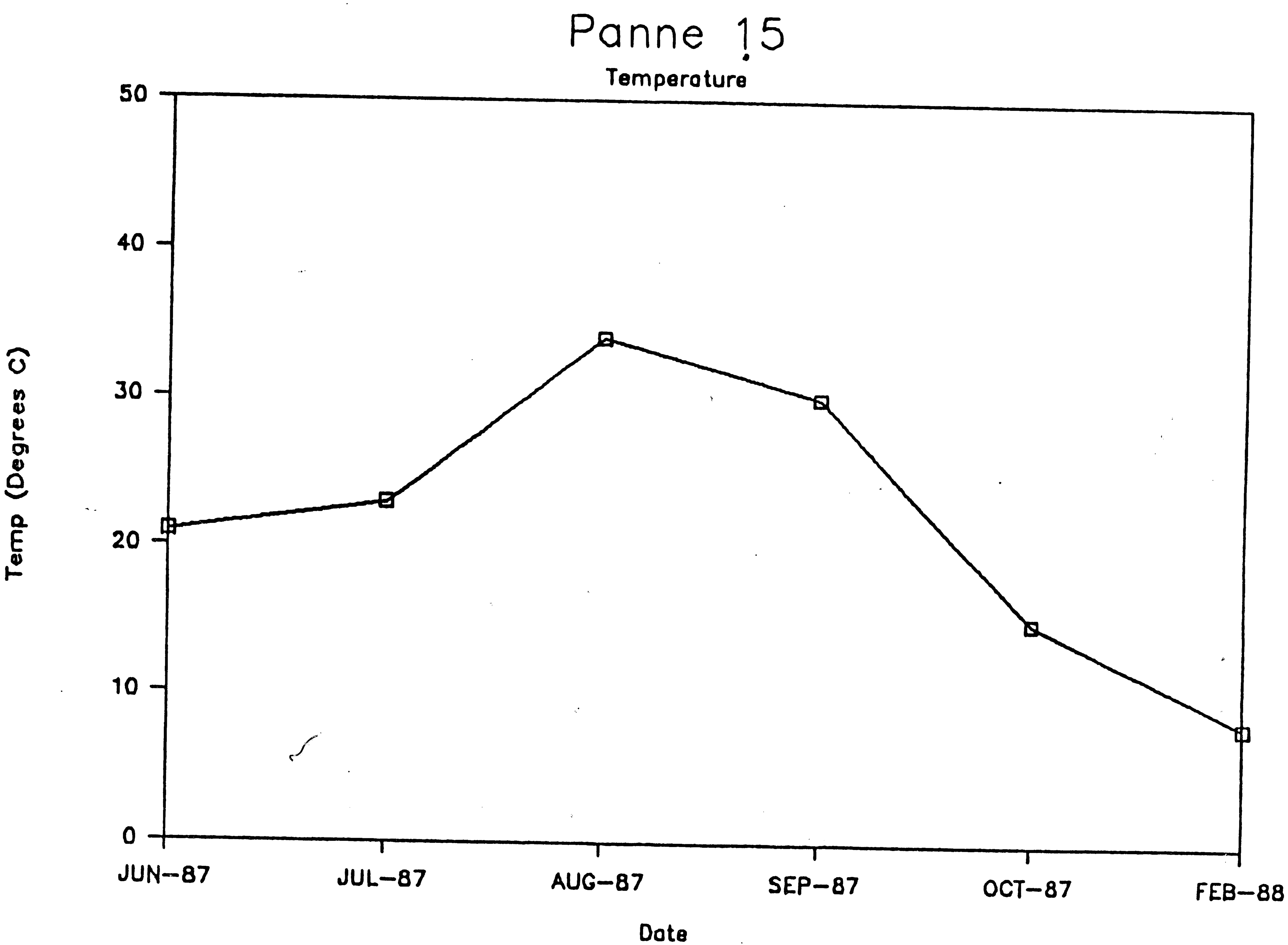

Panne 12
Temperature
50
40
30
20
10
0
Temp (Degrees C)
JUN-87
JUL-87
AUG-87
SEP-87
OCT-87
FEB-88
Date


Panne 13
Temperature
Temp (Degrees C)
0
10
20
30
40
50
JUN-87
JUL-87
AUG-87
SEP-87
OCT-87
FEB-88
Date

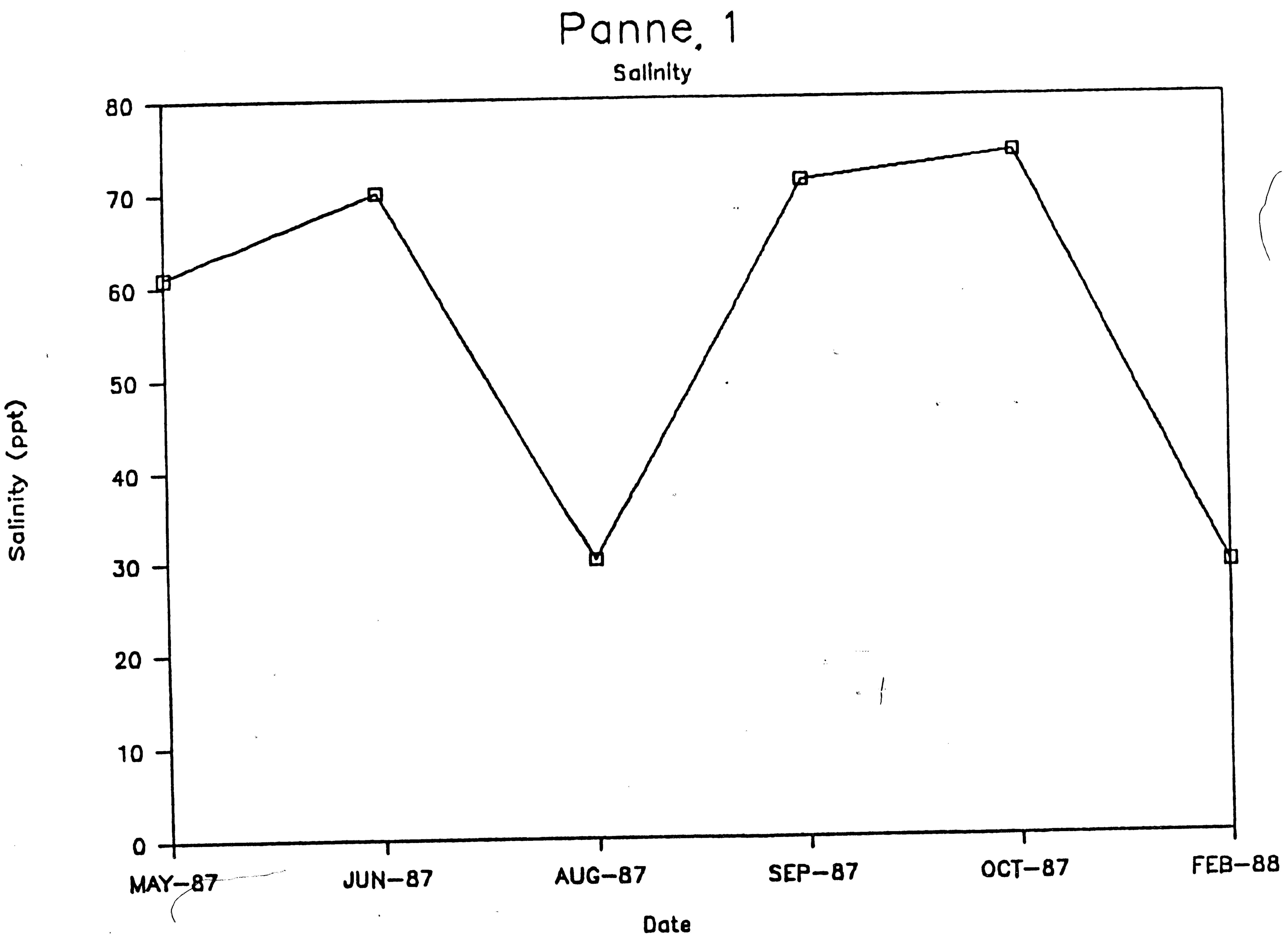
Panne 14

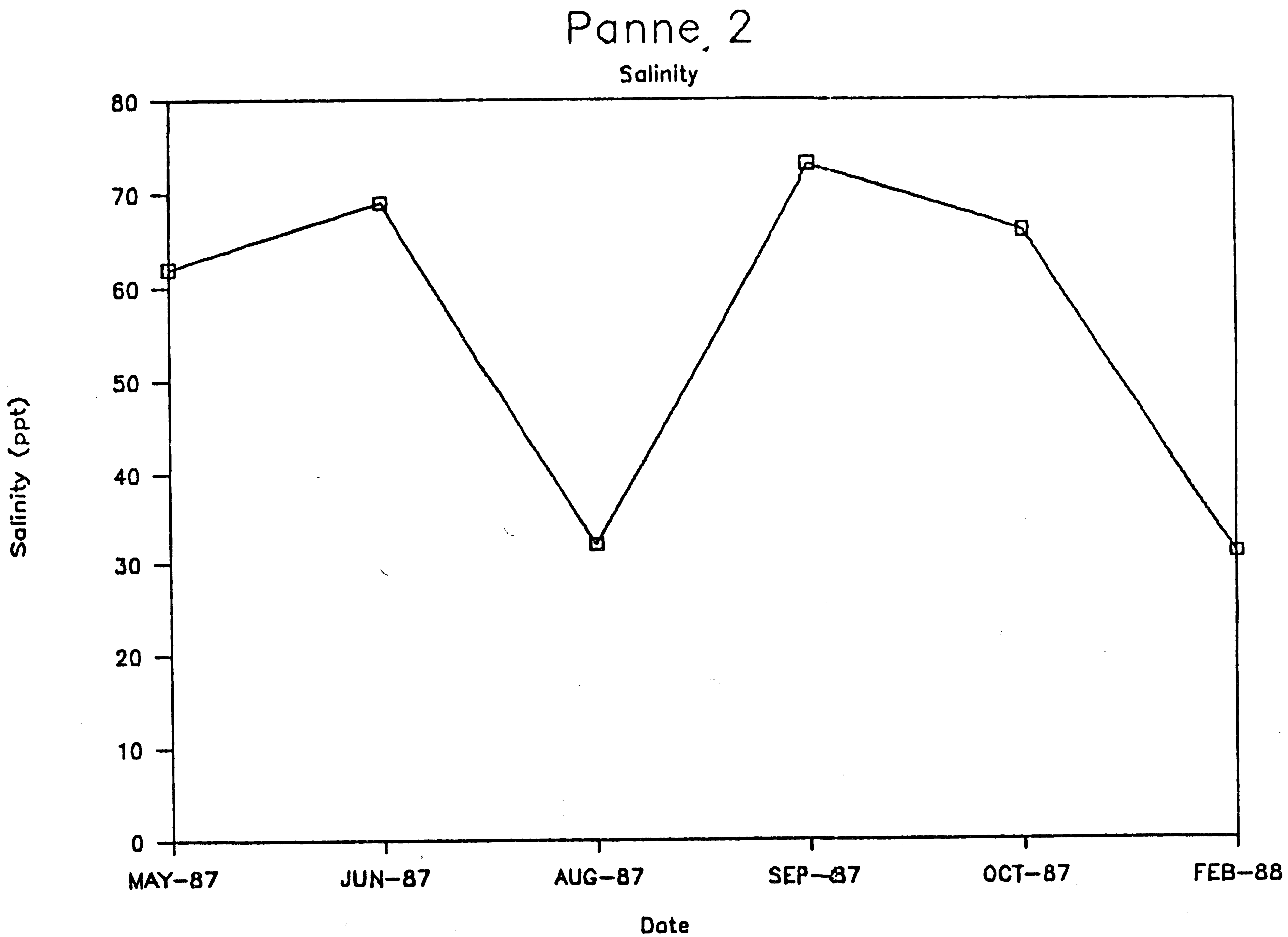
Temperature

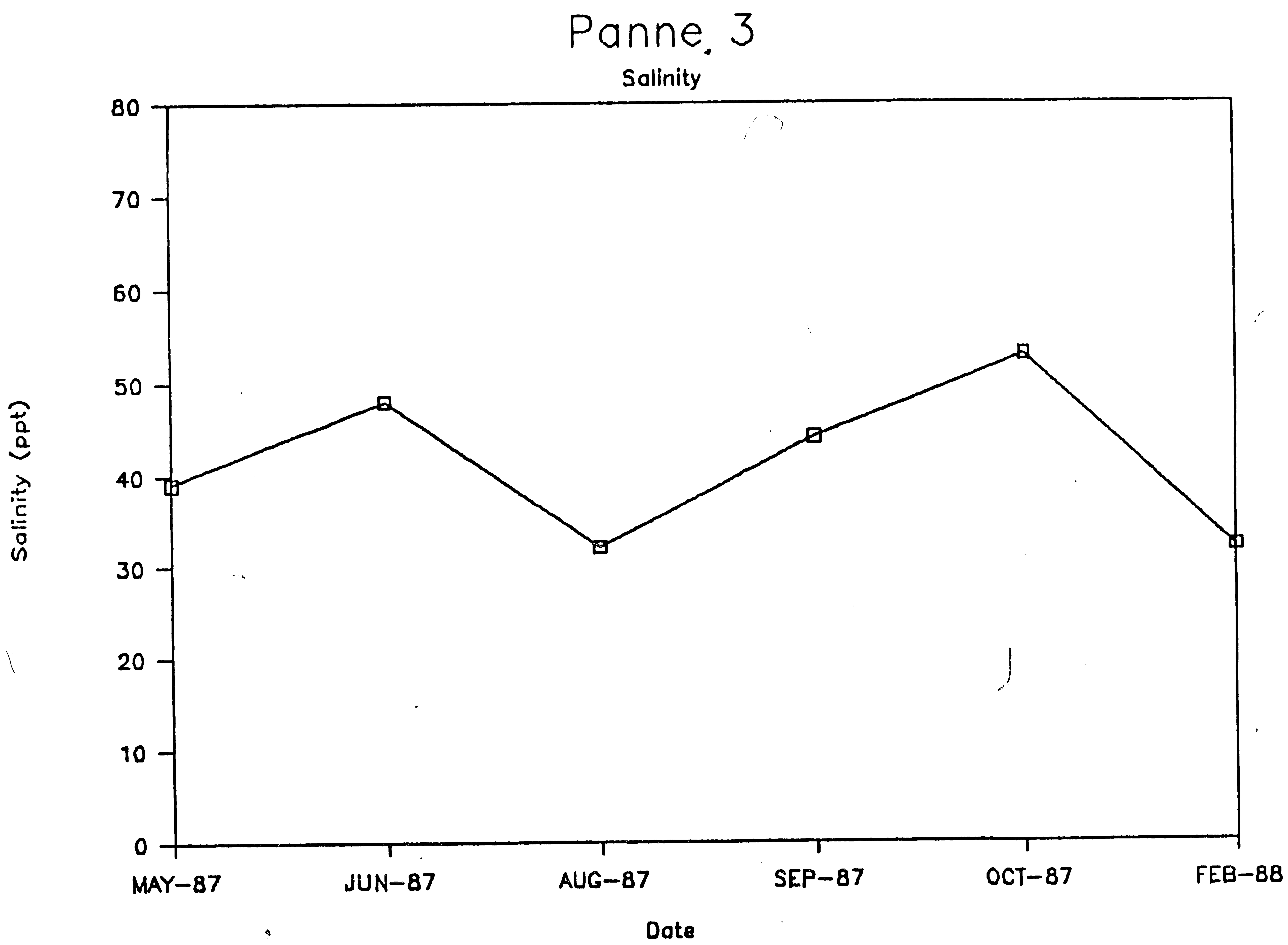




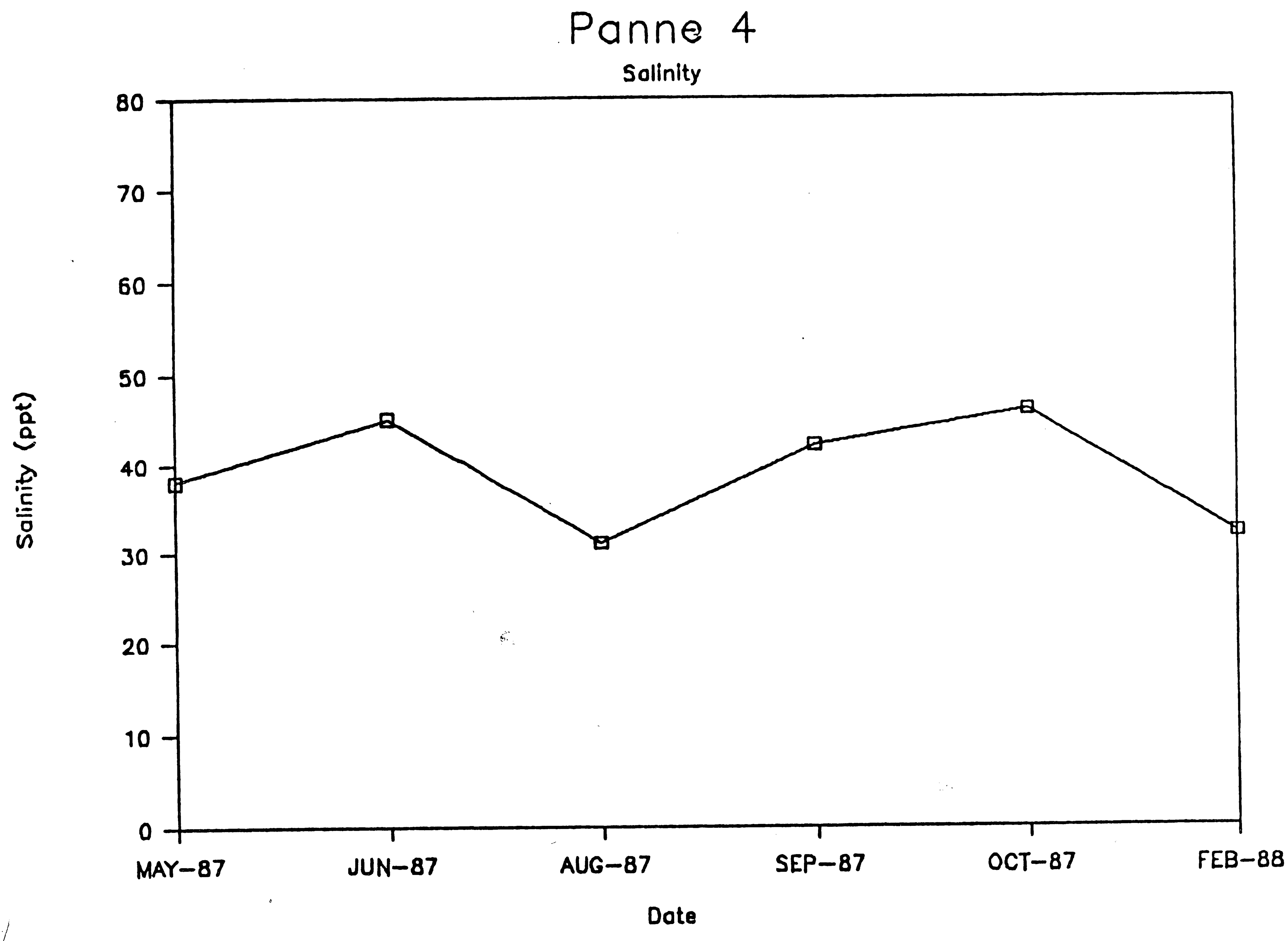
Panne 15
Temperature
Temp (Degrees C)
0
10
20
30
40
50
JUN-87
JUL-87
AUG-87
SEP-87
OCT-87
FEB-88
Date

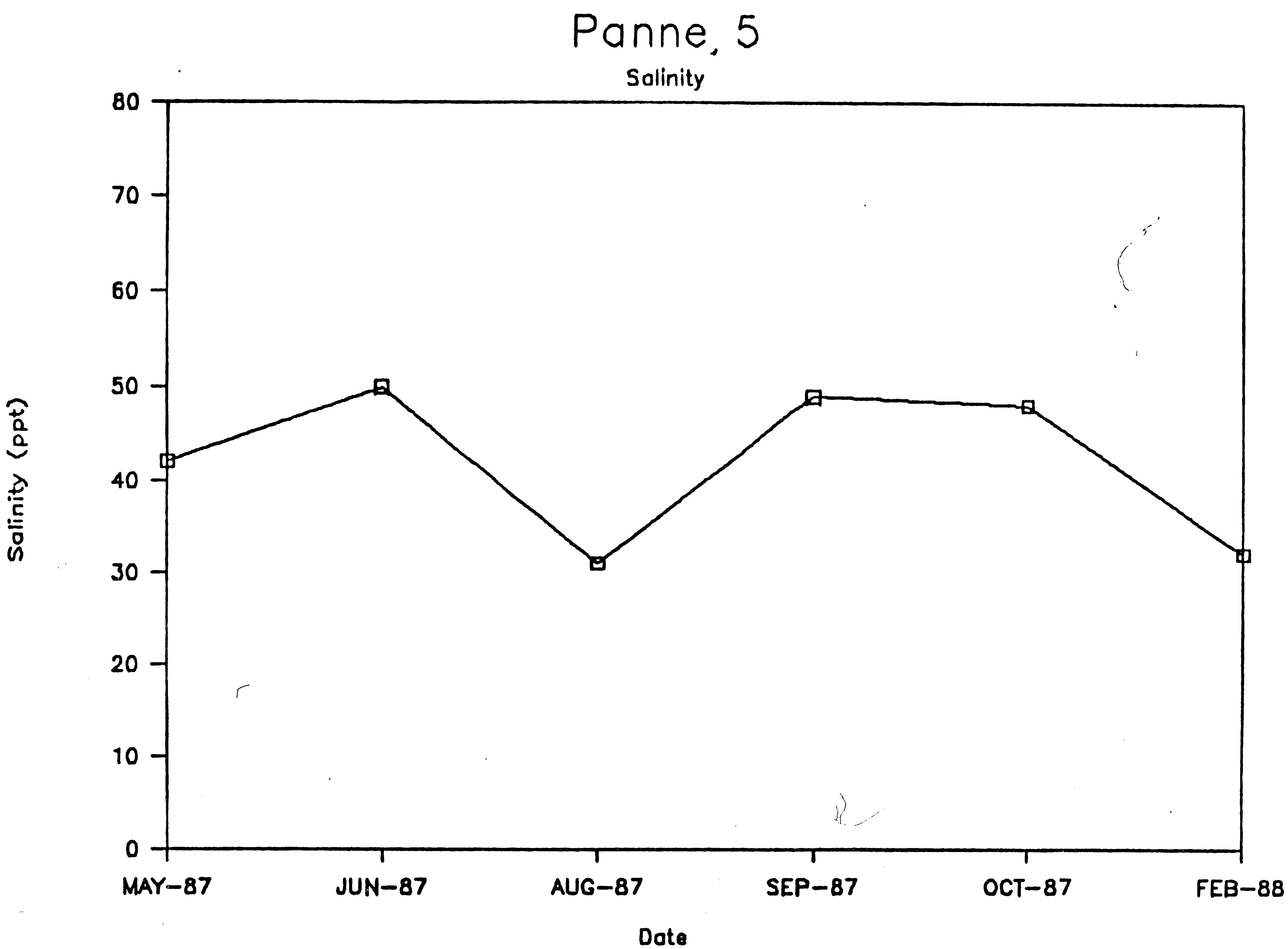

Panne, 1
Salinity
Salinity (ppt)
80
70
60
50
40
30
20
10
0
MAY-87
JUN-87
AUG-87
SEP-87
OCT-87
FEB-88
Date


Panne 2
Salinity
Salinity (ppt)
0
10
20
30
40
50
60
70
80
MAY-87
JUN-87
AUG-87
SEP-87
OCT-87
FEB-88
Date

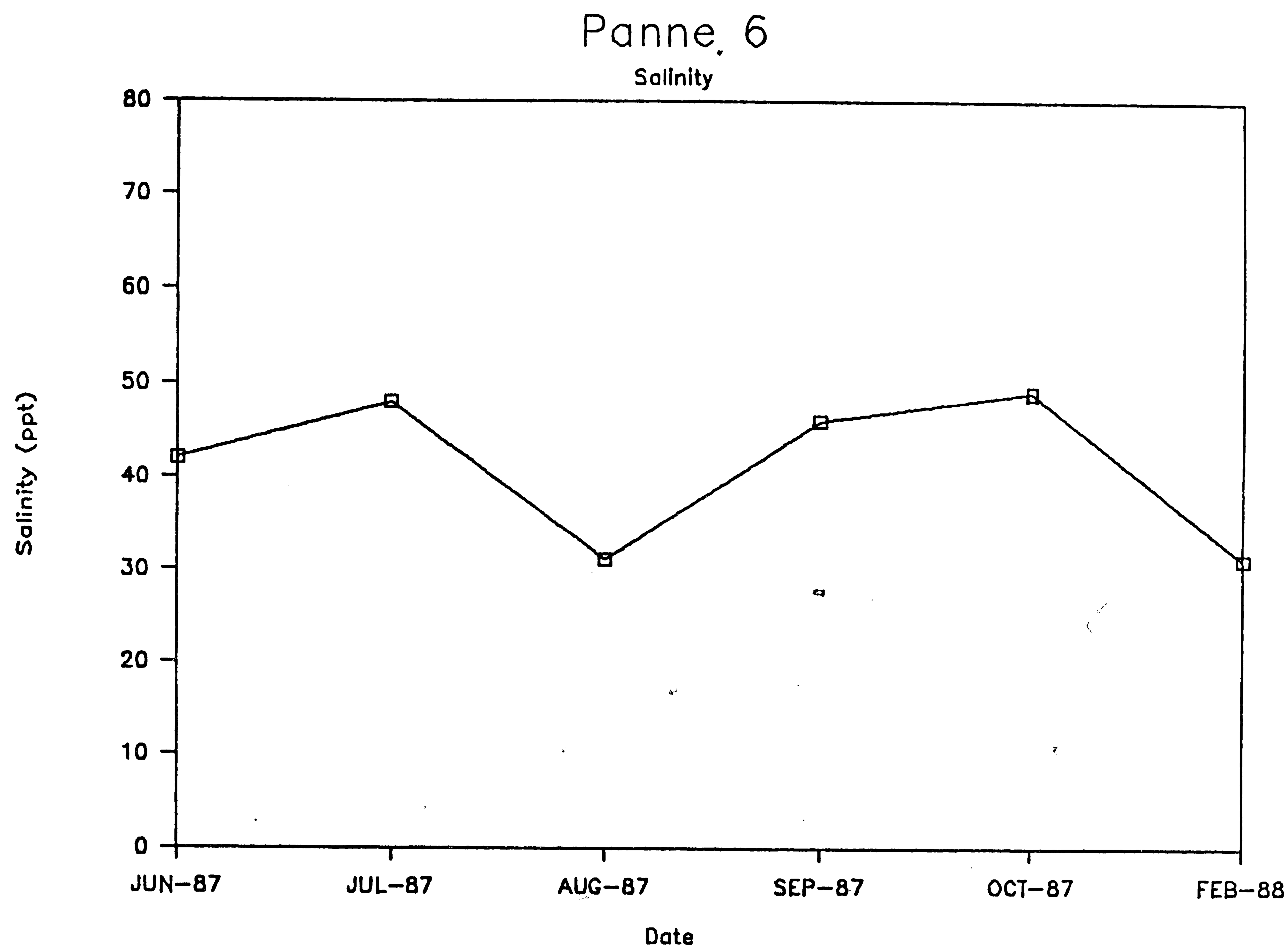


Panne 3
Salinity
Salinity (ppt)
0
10
20
30
40
50
60
70
80
MAY-87
JUN-87
AUG-87
SEP-87
OCT-87
FEB-88
Date

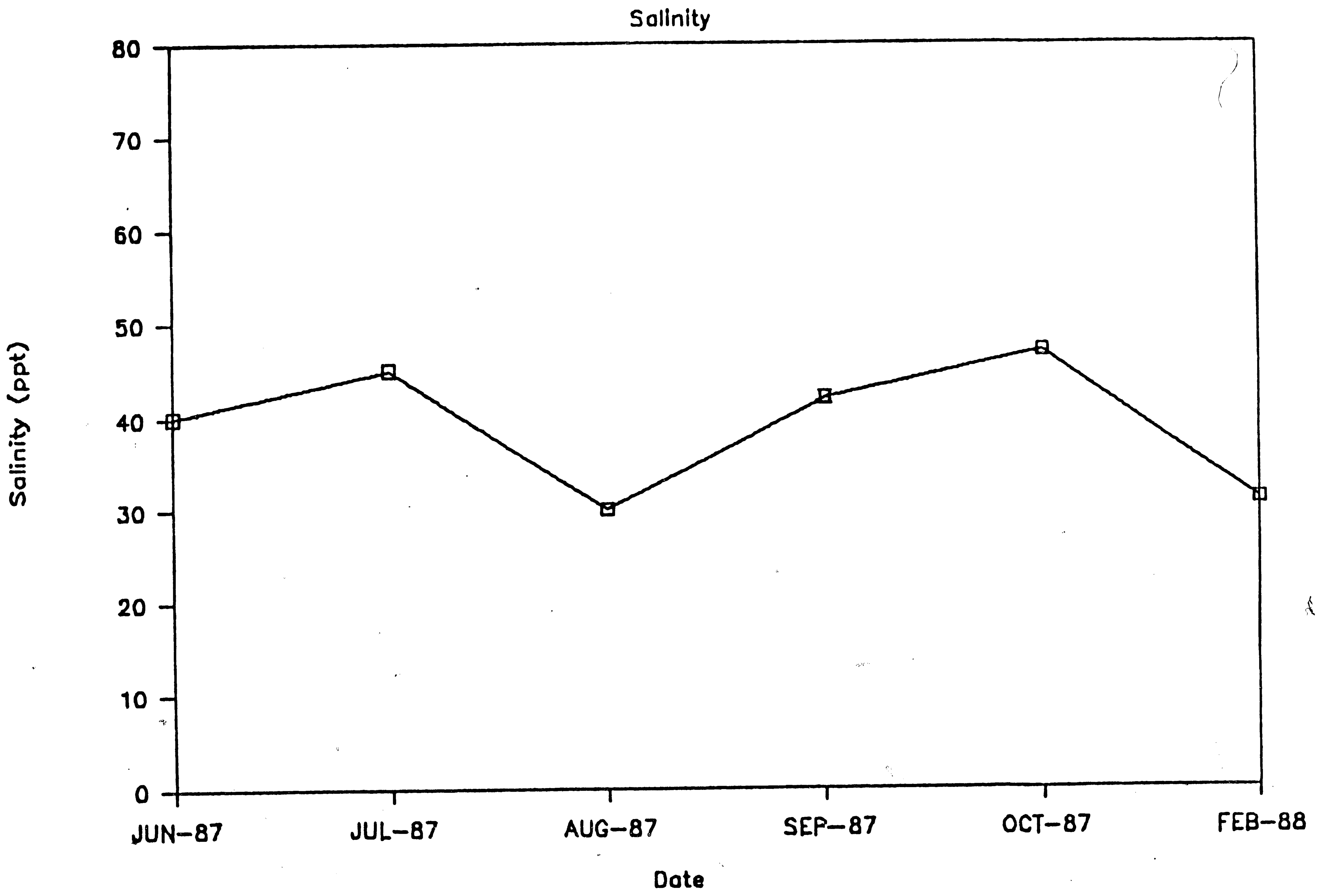

Panne 4
Salinity
80
70
60
50
40
30
20
10
0
Salinity (ppt)
MAY-87
JUN-87
AUG-87
SEP-87
OCT-87
FEB-88
Date



Panne, 5
Salinity
80
70
60
50
40
30
20
10
0
Salinity (ppt)
MAY-87
JUN-87
AUG-87
SEP-87
OCT-87
FEB-88
Date

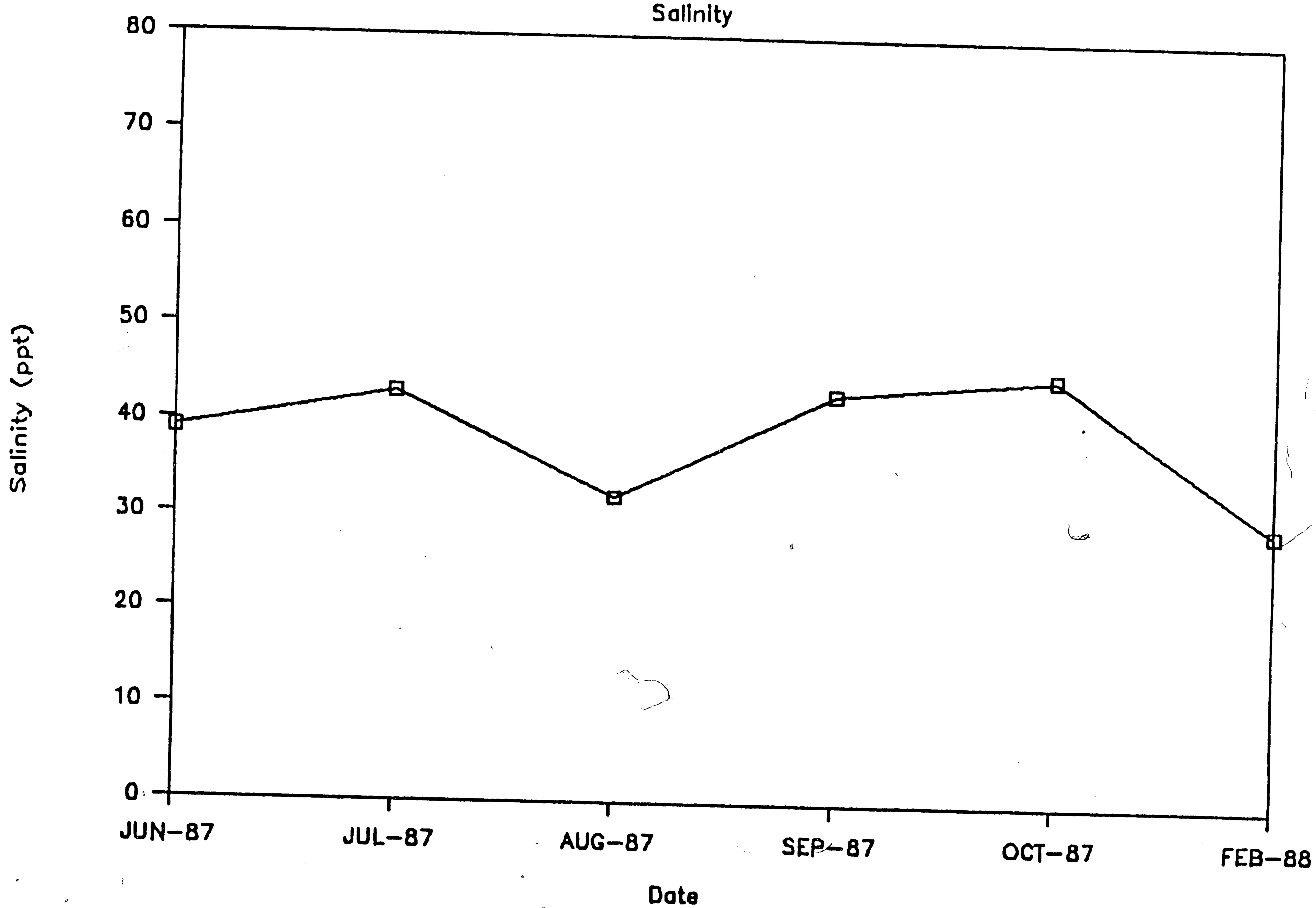

Panne 6
Salinity
Salinity (ppt)
80
70
60
50
40
30
20
10
0
JUN-87
JUL-87
AUG-87
SEP-87
OCT-87
FEB-88
Date

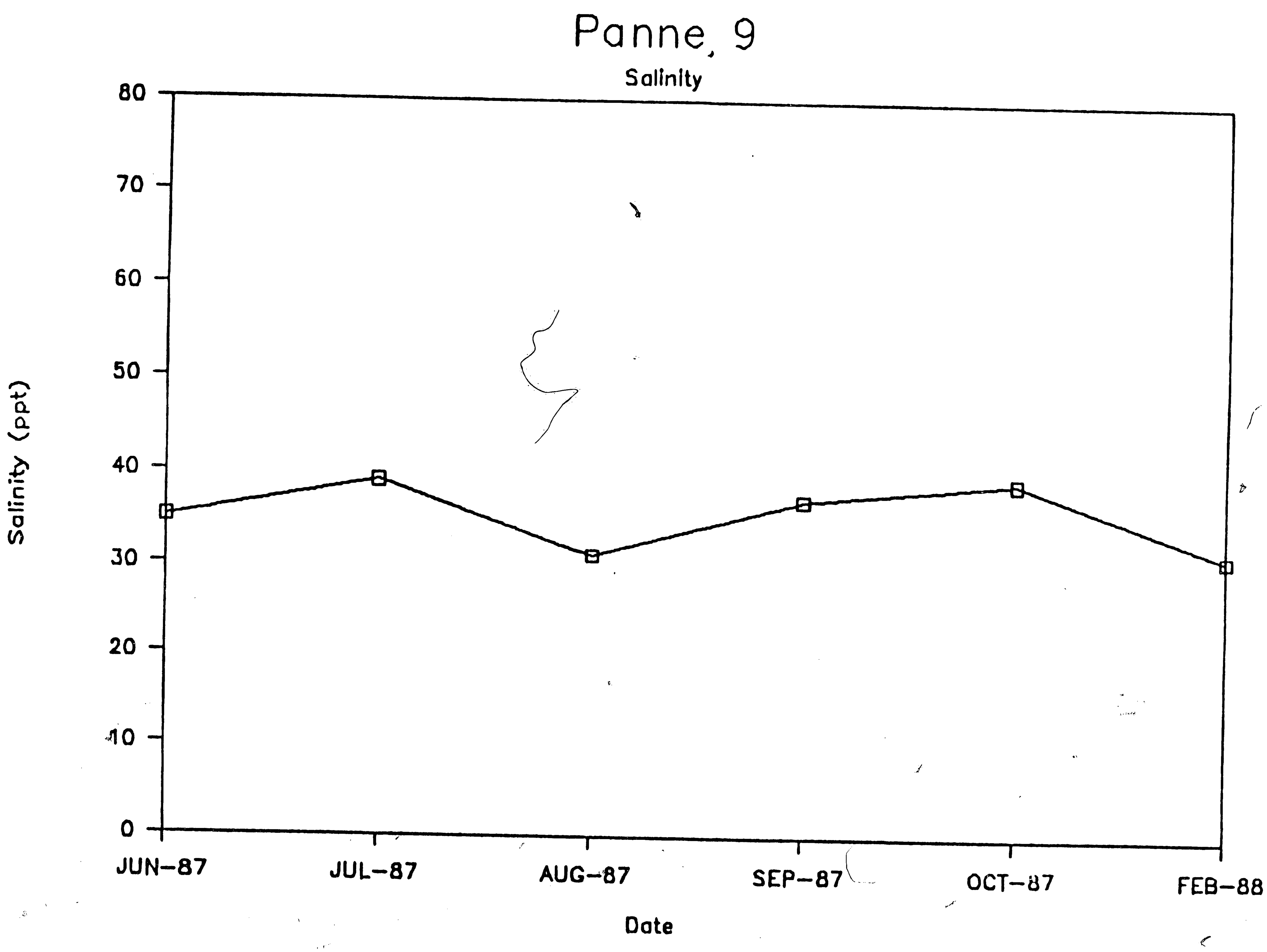
Panne 7


Salinity
Salinity (ppt)
80
70
60
50
40
30
20
10
0
JUN-87
JUL-87
AUG-87
SEP-87
OCT-87
FEB-88
Date

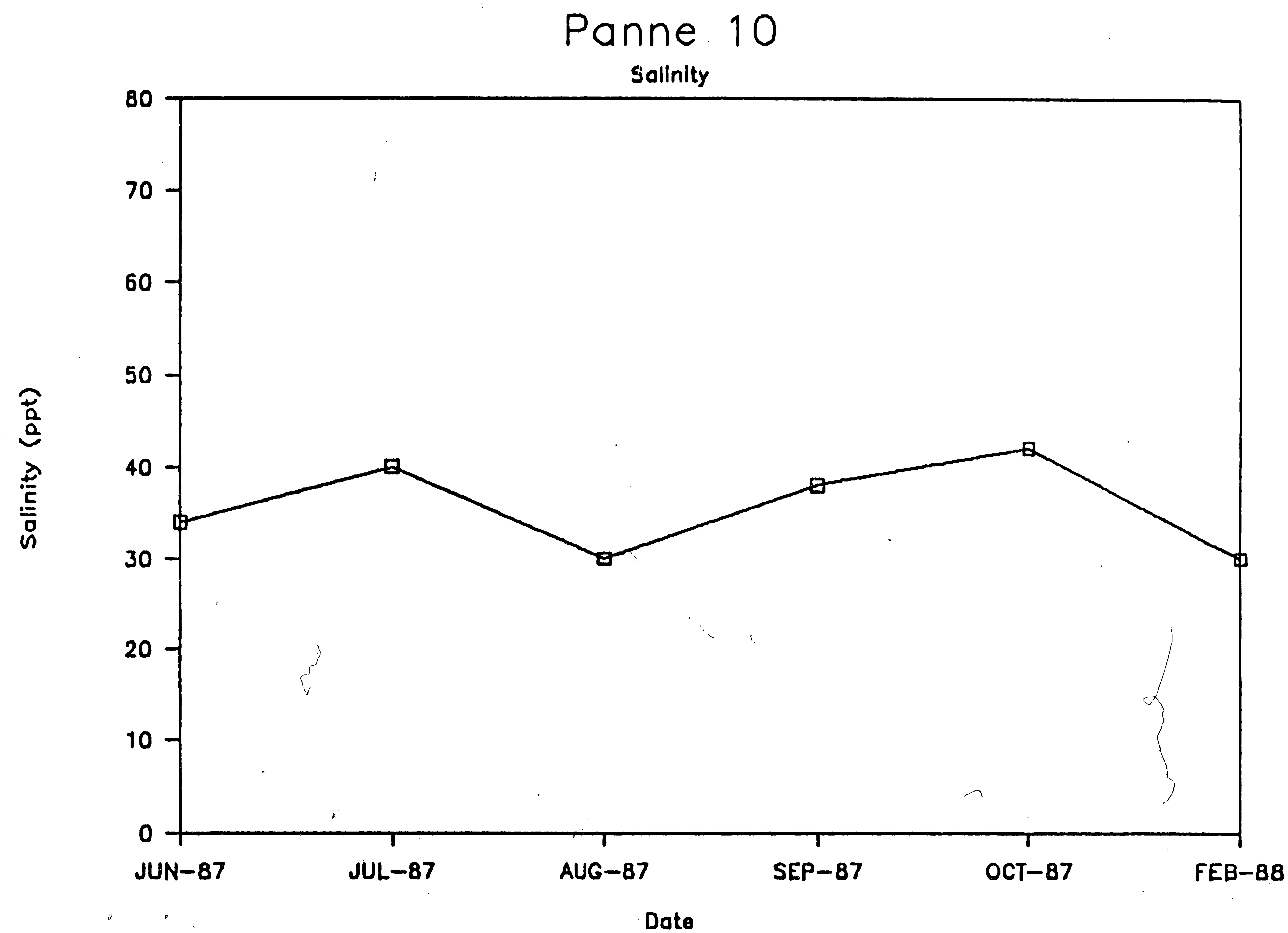
Panne, 8

Salinity

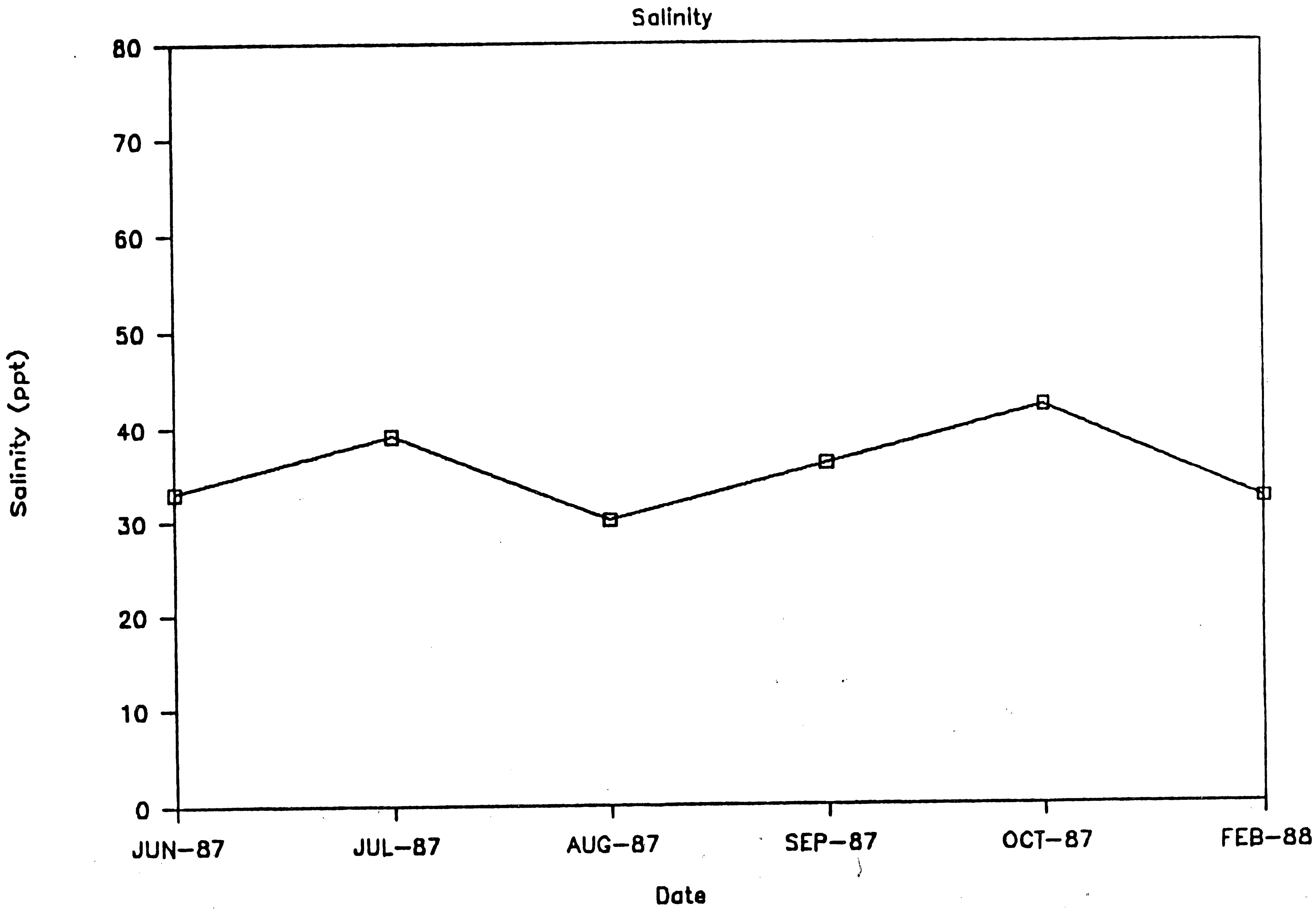




Panne, 9
Salinity
80
70
60
50
40
30
20
10
0
Salinity (ppt)
JUN-87
JUL-87
AUG-87
SEP-87
OCT-87
FEB-88
Date

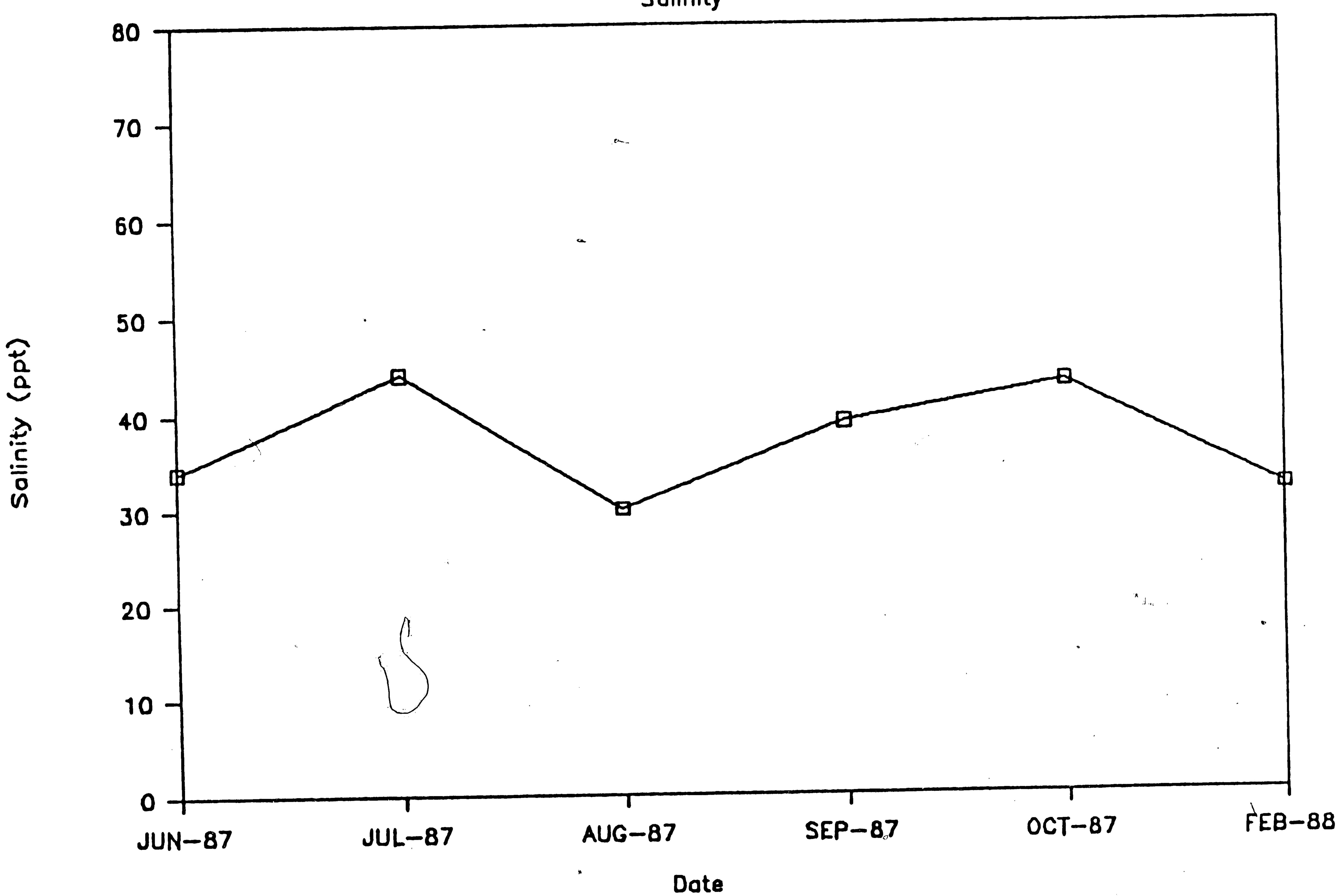

Panne 10
Salinity
80
70
60
50
40
30
20
10
0
Salinity (ppt)
JUN-87
JUL-87
AUG-87
SEP-87
OCT-87
FEB-88
Date

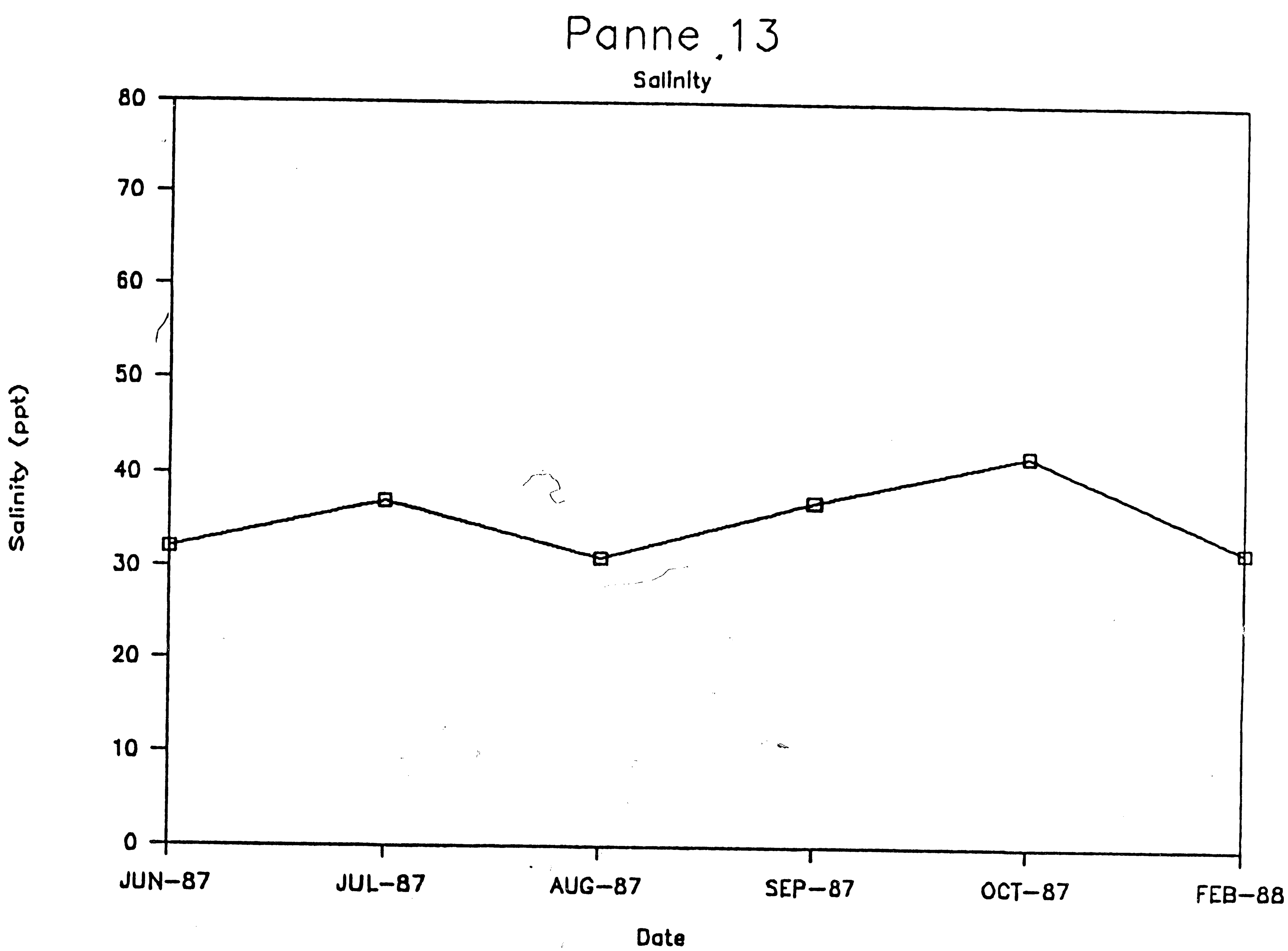
Panne 11


Salinity
Salinity (ppt)
80
70
60
50
40
30
20
10
0
JUN-87
JUL-87
AUG-87
SEP-87
OCT-87
FEB-88
Date

Panne 12

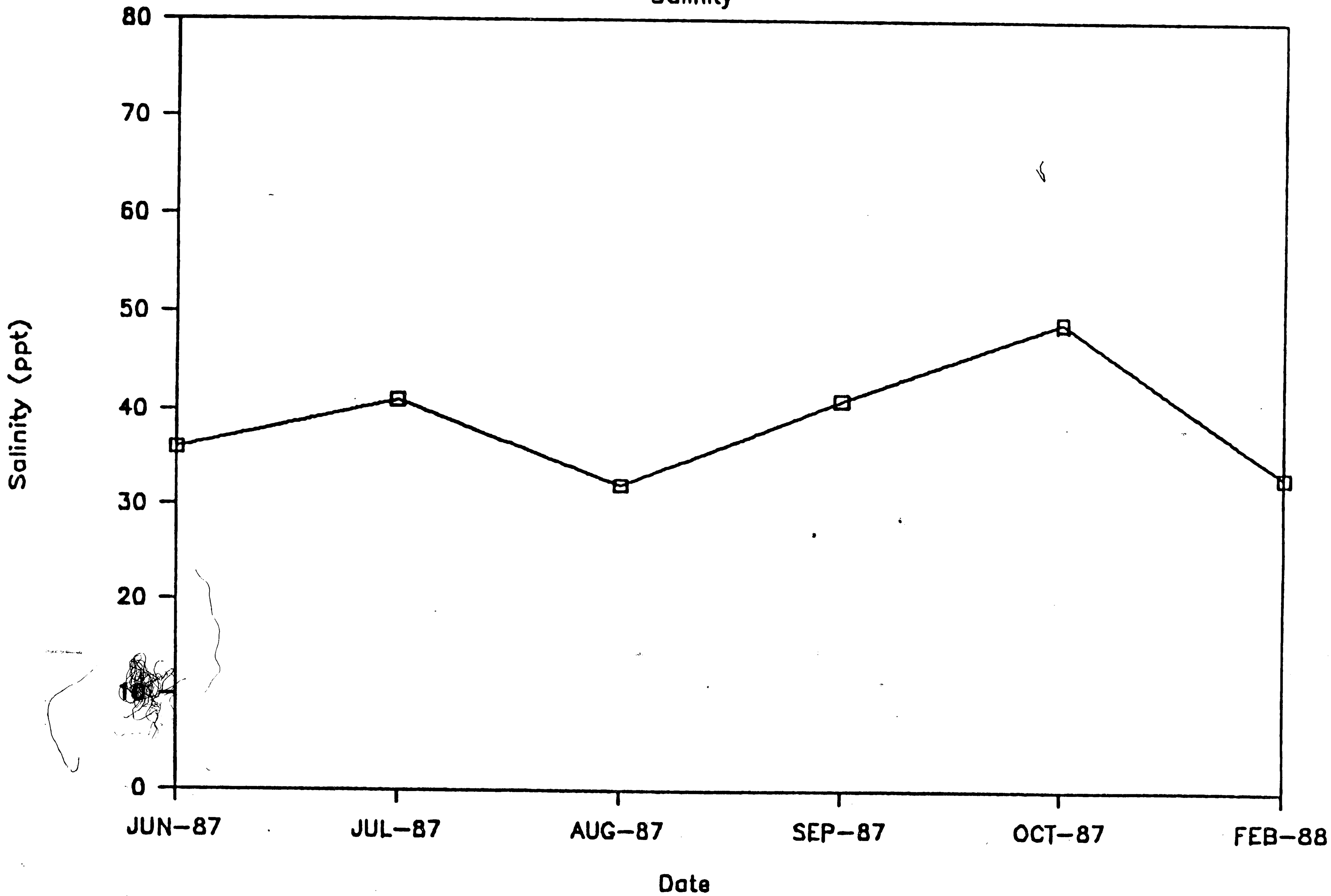
Salinity

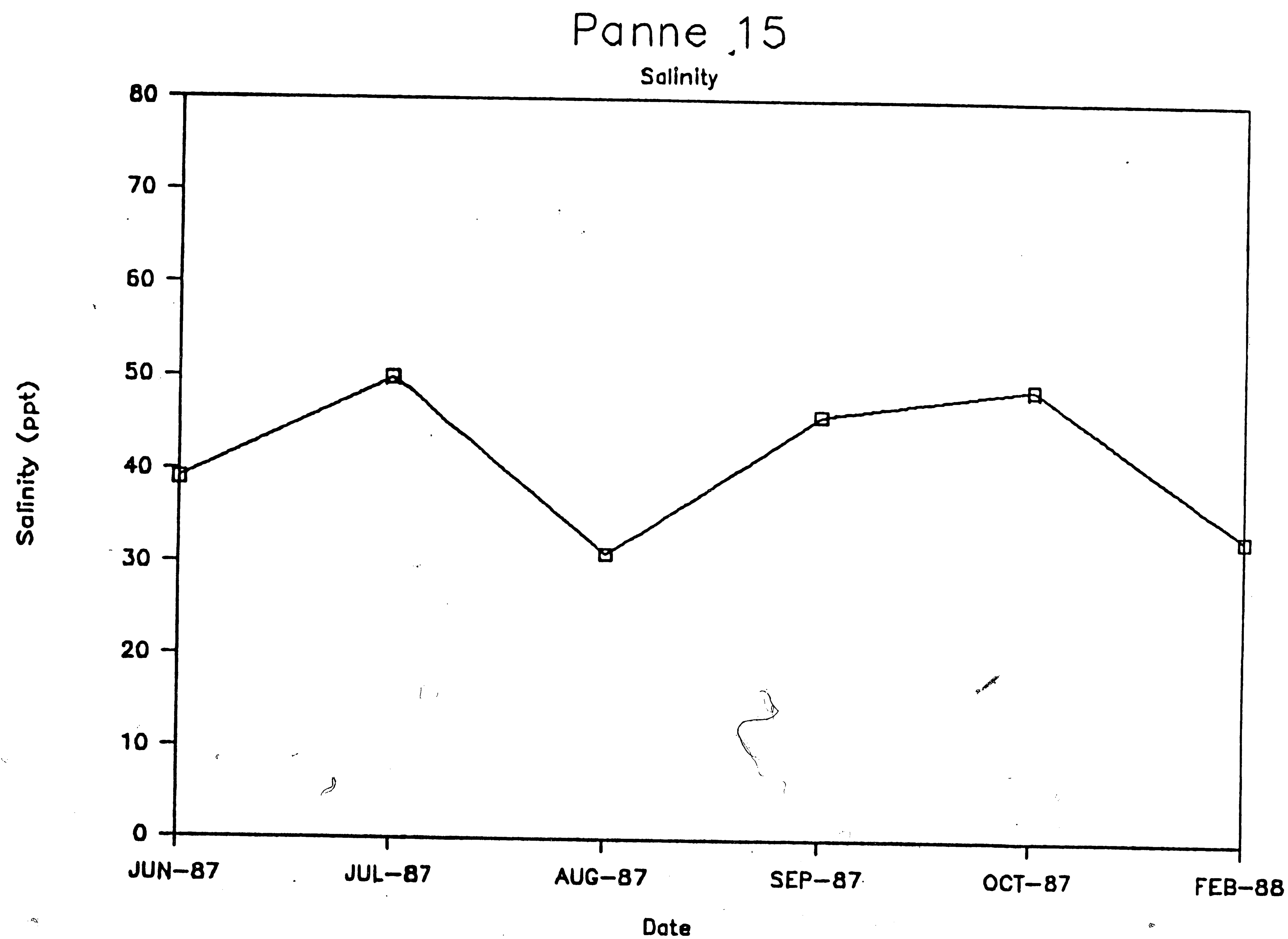



Panne 13
Salinity
Salinity (ppt)
80
70
60
50
40
30
20
10
0
JUN-87
JUL-87
AUG-87
SEP-87
OCT-87
FEB-88
Date

Panne 14

Salinity




Panne 15
Salinity
Salinity (ppt)
0
10
20
30
40
50
60
70
80
JUN-87
JUL-87
AUG-87
SEP-87
OCT-87
FEB-88
Date

Vitae

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Personal History

Date of Birth: June 24, 1962

Place of Birth: Chester, PA

Parents

Father: Richard C. Harrison

Mother: Sheila M. Diamond

Education

May, 1984 — Geneva College, Beaver Falls, PA
Bachelor of Science degree in Biology with minors in Chemistry and Biblical Studies.

Grade Point Average: 3.52 (4.0 Index)

Honors and Activities: Graduated Cum Laude; Dean's List; Geneva Scholar Award; Student Senate, 1980-1981; Class President, 1981-1982; American Mensa Society.

June, 1984 — Ridley Senior High School, Folsom, PA
College Prep, honors and advanced placement study. Graduated in top 10% of class.

Honors and Activities: National Merit Scholarship, Sun Co.; Honor Roll; Electronics Club, Student Director; Drama Club; Amateur Radio Extra Class License.

Professional Experience

4/85-4/86 — Laboratory Technician, DuPont Company, Engineering Testing Center, Waste Water Lab, Newark, DE, Via Work Force Co.