

**Factors affecting the abundance and distribution
of estuarine zooplankton, with special reference
to the copepod Eurytemora affinis (Poppe)**

Thesis submitted for the degree of PhD

Brian D. Roddie

September 1988



IMAGING SERVICES NORTH

Boston Spa, Wetherby
West Yorkshire, LS23 7BQ
www.bl.uk

BEST COPY AVAILABLE.

VARIABLE PRINT QUALITY



IMAGING SERVICES NORTH

Boston Spa, Wetherby
West Yorkshire, LS23 7BQ
www.bl.uk

BEST COPY AVAILABLE.

**TEXT IN ORIGINAL IS
CLOSE TO THE EDGE OF
THE PAGE**

IMAGING SERVICES NORTH

Boston Spa, Wetherby

West Yorkshire, LS23 7BQ

www.bl.uk

TEXT CUT OFF IN THE
ORIGINAL



IMAGING SERVICES NORTH

Boston Spa, Wetherby

West Yorkshire, LS23 7BQ

www.bl.uk

PAGE NUMBERING AS ORIGINAL

Abstract

Factors affecting the abundance and distribution of littoral estuarine zooplankton were investigated by means of both field and laboratory studies.

In the field, a 12-month survey was conducted at 6 stations spanning a wide salinity range in the Forth estuary, to investigate the influence of geographical, seasonal, tidal and physical environmental variables on community structure. Pump samples in two net fractions (69 μm and 250 μm) were collected on spring and neap tides, at high and low water over 9 complete or partial lunar cycles.

The use of two concentric nets of differing mesh size extended the size range of specimens caught, and permitted the observation and enumeration of small plankters such as rotifers, copepod nauplii and early polychaete larvae. In early 1982, a clear temporal succession of rotifers > freshwater crustacea > Maranzelleria larvae > Eurytemora was observed.

The data acquired on field distribution and abundance were analysed in a variety of ways. The most effective approach was found to be a combination of polythetic, divisive classification (Twinspan) of species data, followed by Multiple Discriminant Analysis (MDA) of the classification using geographical, seasonal, tidal and environmental data as the discriminating variables. The effects of geographical, seasonal and tidal variation were removed by analysing subsets of the

data restricted to one state of a variable at a time; comparison of these restricted analyses with those performed on larger data sets revealed, however, that the relative influence of variables on community structure could be readily discerned even when all variables were considered together. Salinity and geographical position of station were clearly the dominant factors in explaining the species associations defined by classification analysis; organic suspended particulate material was closely associated with these, and temperature also but to a lesser degree. The influences of season and primary production were linked, and were orthogonal to the influence of the dominant variables.

Classification analysis identified three main assemblages: the freshwater community; a low-salinity group comprising Eurytemora affinis and Neomysis integer; A neritic assemblage dominated by Acartia spp., Pseudocalanus and Oithona but also including Temora, Centropages and meroplanktonic larvae. Pseudocalanus and Oithona were more persistent than the other neritic taxa, and were more often found in samples of lower salinity and in the autumn and winter.

Predation and development rate are two biological factors which directly influence the abundance and distribution of individual taxa. In the laboratory, studies were conducted a) on the rate of predation of Neomysis on Eurytemora and b) the effects of temperature and food availability on the development rate of Eurytemora.

Predation rates of adult mysids on adult Eurytemora were estimated to

range up to 170 prey/day at 500 prey/litre, and the functional response was adequately modelled by a Type II curve. It was experimentally demonstrated that predation rates were not reduced in the dark or in the presence of detritus, and it is inferred from this that Neomysis relies on random foraging rather than on visual predation. Estimated predation rates were sufficiently high to suggest that Neomysis predation may, at some times of the year, have a significant effect on Eurytemora population size.

Development rates in Eurytemora were not affected by food level, but were quantitatively related to temperature. Development was approximately isochronal, but the duration of the second naupliar instar was consistently longer than that of other instars, especially at lower temperatures. Total estimated development times ranged from 39 days at 8 deg.C to 15.25 days at 20 deg.C, with the effect of temperature being more marked at low temperatures than at high temperatures.

The results of the development study were applied to field observations of instar body lengths, in order to estimate daily length increment for 9 dates in 1982. Field observations had indicated that, in contrast to many other studies, body size did not bear a simple inverse relationship to water temperature; whilst the smallest animals were observed during the spring bloom and midsummer, the largest specimens were collected in September when water temperatures were still high.

Highest growth rates were estimated for August (small animals) and September (large animals) ; winter animals, although similar in size to September specimens, had low estimated growth rates. The large size

of specimens encountered in September suggests, when considered in conjunction with the low abundance at that time, that a switch may have occurred from investment in reproduction to an investment in somatic growth.

GLOSSARY OF ABBREVIATED TERMS USED IN TEXT

Taxon	Authority	% occurrence	Identifier
<i>Eurytemora affinis</i>	(Poppe)		
Adult		81.1	EAFF ADUL
copepodite		89.4	EAFF COPE
Nauplii		85.0	EAFF JUVE
Harpacticid copepods		85.0	HARP SPEC
Rotifera		73.1	ROTI SPEC
(mainly <i>Synchaeta</i> sp.)			
Copepod nauplii (unidentified)		73.6	COPE NAUP
<i>Neomysis integer</i>	(Leach)	20.7	NEOM INTE
<i>Diaptomus gracilis</i>	Sars	24.2	DIAP GRAC
<i>Daphnia</i> sp.		13.2	DAPH SPEC
<i>Bosmina</i> sp.		18.5	BOSM SPEC
<i>Chydorid</i> spp.		4.0	CHYD SPEC
<i>Cyclopoid</i> spp.		10.6	CYCL SPEC
<i>Acartia bifilosa inermis</i>	Rose	20.3	ACAR INER
<i>Acartia tonsa</i>	Dana	15.4	ACAR TONS
<i>Acartia longiremis</i>	Lilljeborg	15.9	ACAR LONG
<i>Acartia clausi</i>	Giesbrecht	8.8	ACAR CLAU
<i>Acartia</i> sp. copepodites		46.2	ACAR COPE
<i>Oithona similis</i>	Claus	39.6	OITH SIMI
<i>Pseudocalanus elongatus</i>	(Boeck)	29.5	PSEU ELON
<i>Temora longicornis</i>	(O.F.Muller)	31.3	TEMO LONG
<i>Centropages hamatus</i>	Lilljeborg	11.0	CENT HAMA
<i>Sagitta elegans</i>	Verril	9.7	SAGI ELEG
<i>Oikopleura</i> sp.		6.2	OIKO PLEU
<i>Calanus helgolandicus</i>		4.9	CALA HELG
<i>Littorina littorea</i>	(L.)		
egg capsules		25.5	LITT CAPS
veligers		11.9	LITT VELI
Cirripede nauplii		51.5	CIRR NAUP
cyprids		20.3	CIRR CYPR
Terebellid larvae		10.6	TERE LARV
<i>Polydora</i> larvae		29.5	POLY CILI
<i>Eteone</i> sp. larvae		4.8	ETEO LARV
<i>Maranzelleria wireni</i>			
larvae		22.5	MARA WIRE
eggs		8.4	MARA EGGS
trochophores		7.0	MARA TROC
Bivalve larvae		8.4	BIVA LARV
Aphroditid larvae			APHR LARV

GLOSSARY OF ABBREVIATED TERMS USED IN TEXT

Variable	Shorthand identifier	Transformation
Distance from upper tidal limit	Dist	Log10
Tidal state (H,N etc)	Tide	Dummy 4-state variable
Date	Date	None, represented as decimal month
Inorganic component of suspended solids	Inor	Log10
Organic component of suspended solids	Org	Log10
Organic percentage of suspended solids	Xorg	$\arcsin/\sqrt{\log_{10} X+1}$ (x as proportion)
Salinity	Sal	None
Temperature	Temp	None
Chlorophyll a	Chl a	Log10
Acid Ratio	AR	Log10
Phaeopigments	Phae	Log10
Freshwater discharge at upper tidal limit	Disch	None

Contents

Introduction

Chapter 1 Field survey of littoral estuarine zooplankton and associated environmental variables	1
--	---

Materials and Methods

Sampling equipment	1
Calibration and testing	2
Sampling programme	3
Sampling	9
Estimation of small-scale temporal and spatial variability	10
Zooplankton sample processing	13
Numerical analysis of survey data	17
Multivariate analyses	17
Relationship between community structure and environmental, spatial and temporal variables	19
Water samples	21
Results	23
Environmental variables	23
Temperature and salinity	24
Suspended solids and photosynthetic pigments	30
Comparative trends	38
Zooplankton	41
Taxa recorded and frequency of occurrence	41
Distribution of taxa in samples	43
Spatial and temporal patterns of abundance in individual taxa	48

Patchiness	54
Spatial variation	54
Temporal variation	57
<u>Eurytemora affinis</u>	58
Effects of preservation	58
Variation in length	58
Abundance	65
Age structure	77
Multivariate analysis of field survey data	91
Environmental variables	91
Environmental data	93
Taxa included	94
Samples categorised by station	101
Samples categorised by sampling cycle	135
Samples categorised by tidal state	162
Chapter 2 Measurements of development rate in <u>E.affinis</u>	
Material and Methods	181

Experiment 1: development rates in mass culture at 15 and 20 deg.C	181
Experiment 2: development rates at four temperature and two food levels	184
Results	189

Experiment 1: development rates in mass culture	189
Experiment 2: development rates at four temperatures and two food levels	191

Primary production	191
Comparison of development and survival between replicates and food levels	191
Estimation of egg development times	193
Estimation of naupliar and copepodite development rates	194
8 deg.C	194
12 deg.C	199
16 deg.C	205
20 deg.C	210
Average stage duration	210
Development rate as a function of temperature	218
Estimation of daily length increment from field and lab. observations	220

Chapter 3 Predation by Neomysis integer on Eurytemora affinis

<u>Materials and Methods</u>	227
Collection of experimental material	228
Pretreatment and exposure of mysids	229
a) effects of size on predation rate	229
b) estimation of functional response	231
c) predation in the dark and in the presence of detritus	232
Sorting and preparation of copepods	233

Results 235

Relationship between size and predation rate 238
Functional response 242
Predation in presence of detritus 253
Foraging in the absence of light 255

Discussion

Field survey 257

Equipment performance 257

Taxa identified 257

Community structure and environmental variables 260

Chi-squared test of association between taxa and samples 261

Classification 262

Assessment of methods 266

Patchiness 268

Dunmore 268

Skinflats 268

Eurytemora affinis 269

Predation 269

Development rates 271

Field observations 274

Summary 277

Introduction

The zooplankton of estuaries has been widely studied (e.g. Miller 1983, Collins and Williams 1982, Taylor 1987) and their characteristics described. The estuarine environment poses particular problems for zooplankton, both physiological and behavioural. Lance (1965) has demonstrated that osmoregulatory ability may influence species distribution, while Burkill et al (1982) and dePauw (1973) inter alia have suggested that behavioural explanations need to be invoked to explain the maintenance of endemic populations in the face of high flushing rates. For species that can successfully overcome these problems, the low-salinity regions of estuaries may provide a rich resource (Morris et al 1978, Heinle et al 1977) and lead to high secondary production.

A feature of estuaries is often the high proportion of the total area accounted for by the intertidal zone and shallows. Roddie (1980) and dePauw (1973) have demonstrated the importance of the littoral zone as a refuge from flushing, but more information on this habitat is needed in order to understand the extent to which its inhabitants constitute a true community.

The marked gradients present in estuaries (both spatial and temporal) should constitute strong influences on the structure of zooplankton communities. The estuarine habitat should therefore

be a suitable environment in which to test methods for resolving and interpreting community structure.

A difficulty in understanding the structure of species assemblages lies in objectively relating a complex of environmental variables to a complex of species. A wide variety of classification and ordination methods are available for uncovering species association. One aim of the present study was to apply combinations of some of these methods to establish to what degree the littoral estuarine plankton of the Forth possess discernible structure, and to what degree this structure could be quantitatively related to physical, spatial and temporal factors. To help achieve this, a sampling programme was designed to cover the major semidiurnal and semilunar cycles on a seasonal basis, and thus to permit variation on a variety of levels to be removed by the analysis of categorical data subsets. The degree to which a method succeeded could then be tested by examining the extent to which samples were sorted by logical category in the analysis.

Biological factors, in addition to environmental factors, act to structure communities. Roddie (1980), Burkill et al (1982), and Heinle and Flemer (1976) have shown that the copepod genus Eurytemora can achieve high abundance at the upper end of estuaries, and Roddie et al (1984) have demonstrated the ability of this species to regulate its haemolymph concentration under conditions of low and fluctuating salinity. Taylor (1987) has characterised the upper estuarine zooplankton of the Forth

estuary as comprising the mysid Neomysis integer and Eurytemora; Heinle and Flemer (1976), Burkill and Kendal (1982) and others have suggested that Neomysis may prey on Eurytemora and this may be an important route of energy transfer from the detrital to the pelagic food web. A second aim in this work was, therefore, to establish if predation did occur, and if so to quantify the process and gain some insight into the potential impact of Neomysis predation on the Eurytemora population.

The maintenance of an indigenous population requires that net population growth rate exceeds the flushing rate of the habitat. One factor influencing population dynamics is the rate of physiological development and maturation (generation time) of a species. Evidence indicates that, in copepods, development rate is both temperature- and food-dependent (Corkett and McLaren 1970; Klein Breteler et al 1984). The third aim of this study was to estimate the effect of temperature on the development of Eurytemora fed on environmentally-realistic concentrations of natural suspended particulate material. Heinle et al (1977) have shown that copepods can grow and reproduce when fed microbially-rich detritus, and Boak and Goulder (1984) have shown that Eurytemora in the Humber estuary can graze on bacteria attached to suspended particulate material. By applying laboratory-derived estimates of development rate to field observations of size distribution at different times of year, it was intended to estimate the daily length increment of each developmental stage at a range of temperatures.

Chapter 1

Field survey of littoral estuarine zooplankton and associated environmental variables

Sampling equipment

The sampling equipment was required to effectively sample small (< 10 mm) zooplankton in shallow water. A previous study (Roddie, 1980) had used concentric 250 μm and 69 μm mesh nets suspended vertically in a wooden frame, the whole assembly being positioned in shallow water so that the net openings were about 20 cm above the water surface. 100 l of water collected with a 10 l bucket was filtered through these nets.

In the present study, it was considered necessary to develop a method which could rapidly sample a larger volume with less disturbance of adjacent water, and which was free of the depth restriction imposed by a wooden frame of fixed height.

Sampling requirements were met by a 12v Teleflex-Morse centrifugal pump with a nominal delivery rate of 100l/min, modified as illustrated in Fig.1.1 . Rigid PVC pipe was connected to the pump outlet to act as a handle and permit sampling in depths of up to 1m. A cone attached to the pump inlet reduced the intake diameter to 2cm . This had the effect of increasing intake velocity (and thus the velocity gradient close to the intake), reducing the likelihood that zooplankton escape responses would be effective in avoiding capture. 2 m of flexible 2.5 cm diameter polythene tubing connected to the rigid pipe delivered water to concentric 250 μm (inner) and 69 μm (outer) mesh nets suspended from a frame attached to expanded polystyrene floats which held the net mouths 15 cm above the water surface. Each net terminated in a 2.5 cm diameter cod end 7.5 cm in length, to the bottom end of which was welded a screen of nylon net of the appropriate mesh size.

Power was supplied to the pump via 10 m of cable by a 12v motorcycle

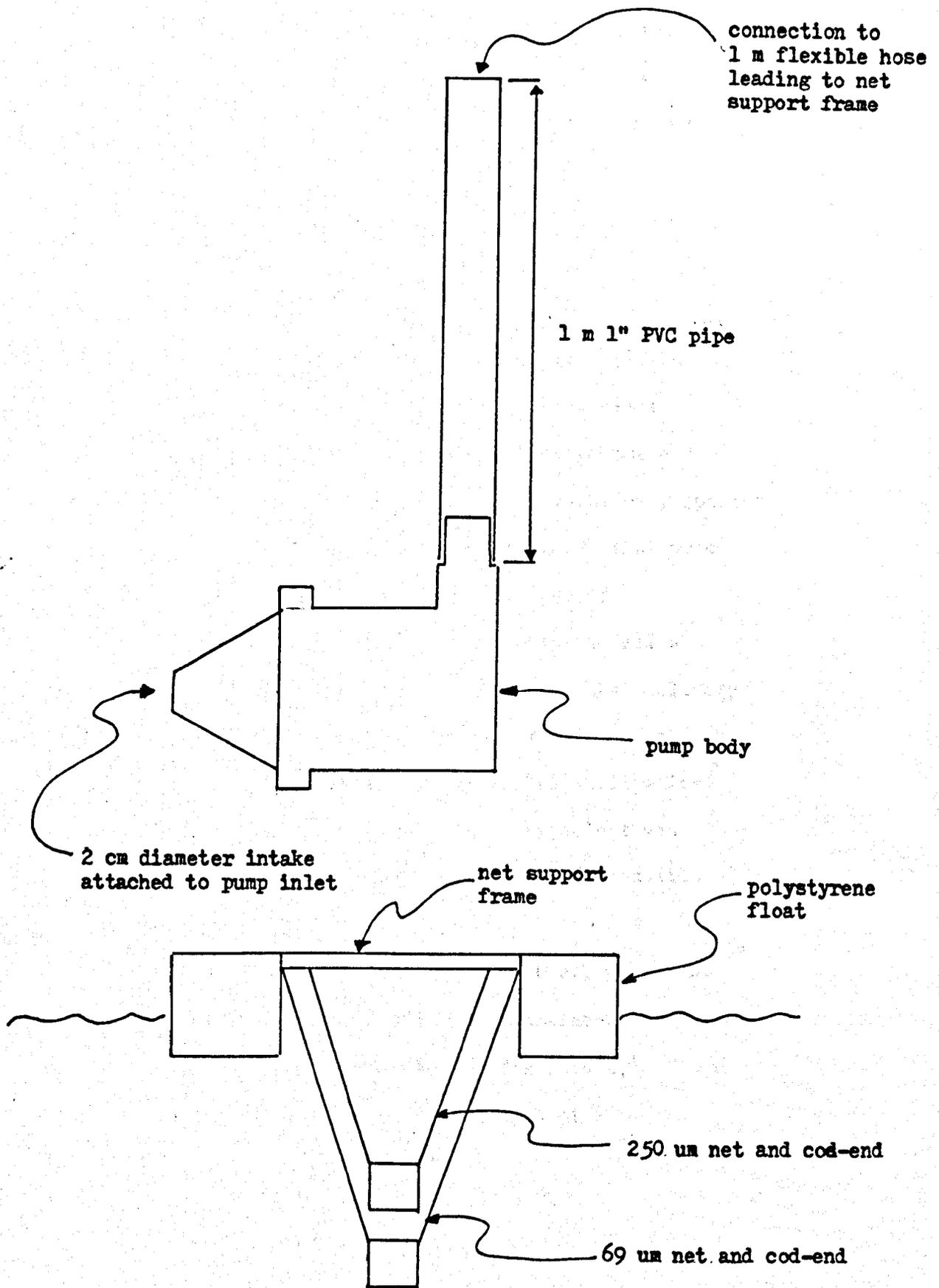


Figure 1.1 Centrifugal pump configuration and concentric net design

battery mounted in a backpack. It was thus possible to operate the sampling equipment in any location which was physically accessible. The pump was activated by a toggle switch mounted on the rigid PVC pipe.

Calibration and testing

The pump was tested to determine whether zooplankton could be sampled without damage, and to establish the most convenient method of calibration. Preliminary sampling was carried out on 30.11.81 at S.Alloa(Fig.1.2). Eurytemora affinis was the only species present. Microscopic examination of the samples revealed that none of the individuals collected had been physically damaged.

Calibration was achieved by recording the time taken to fill a 45 l polythene bucket. Initial measurements indicated that delivery rate varied between 70 and 85 l/min at between 0 and 25 cm head. 25 cm was chosen as the standard elevation above sea surface for the highest point in the delivery system, and every effort was subsequently made to maintain this height as closely as possible during sampling.

Calibration was carried out prior to sampling on every occasion. Assuming a possible error of ± 1 l in volume measurement, and ± 1 s in time measurement, sample volume was thus determined, independently for each sample, with an error(range) of approximately $\pm 5\%$.

Sampling programme

Between December 1981 and December 1982, zooplankton and water samples were collected over a series of lunar cycles at 6 shore sites on the Forth estuary (Fig.1.2, Table 1.1). Sampling was conducted less intensively, at quarterly intervals, in 1983. Four sites (Fallin, S.Alloa, Dunmore and Kincardine) were located in the upper estuary and were characterised by low and variable salinity. Two sites (Culross and Skinflats) were located in the middle estuary and were characterised by relatively higher and more stable salinity (Roddie, 1980). The study of Roddie (1980) was used as a pilot survey in determining the choice of stations. Those chosen represented the full range of estuarine conditions; Fallin had been found to reflect considerable influence of freshwater planktonic communities, while Culross had been found to reflect some influence from coastal communities.

All sites were readily accessible by road, and travel between sites was accomplished by road. Displacement of high and low water at each site was estimated from the tidal simulation models of Frazer et al (1972), and trial runs conducted to establish travel times between sites (Table 1.1). These trials demonstrated the feasibility of sampling all stations on the same tide; in practice, it was possible to follow the tidal pulse up and down the estuary, sampling within 30 min. of high and low water at each of the upper estuary sites and within 30 min. of high water only at the middle estuary sites. The extent of the intertidal zone at the middle estuary sites made low water sampling impracticable.

Variation in the timing of high and low water throughout the year prevented sampling under similar light conditions both within and

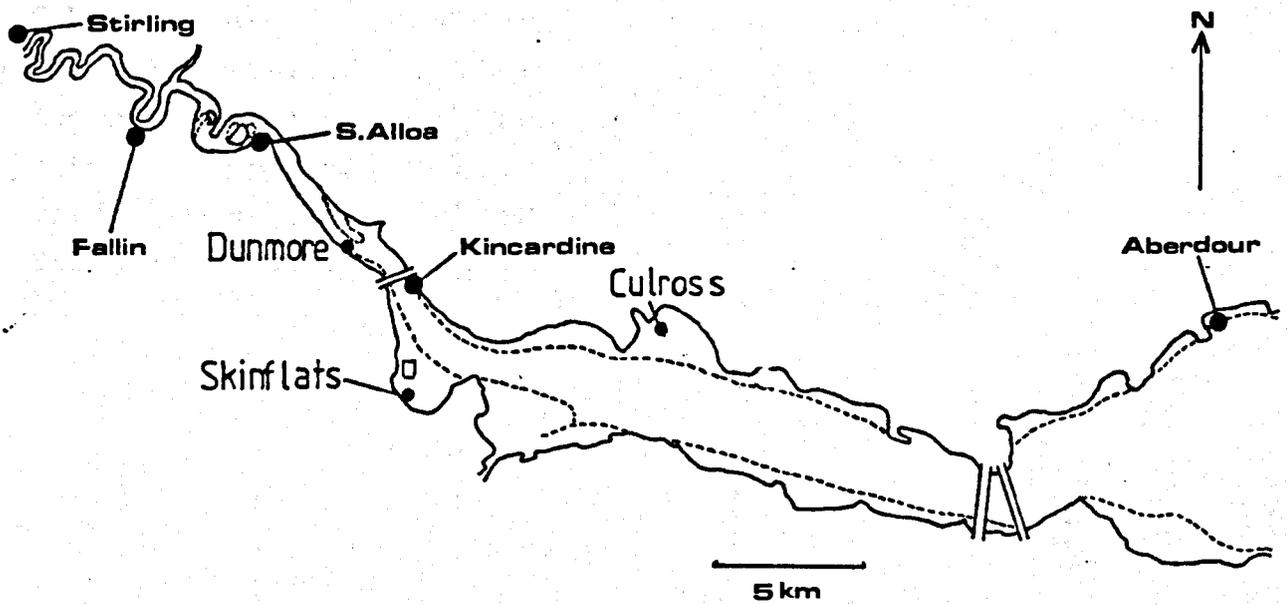


Figure 1.2 The Forth estuary and location of sampling stations

Table 1.1 Tide time corrections for, and travel times between, stations

TIDE TIME CORRECTIONS

(Relative to Rosyth)

Based on model simulations for spring tides by Fraser et al (1972)

	High tide	Low tide
Skinflats	=	-1 hour
Culross	=	-1 hour
Kincardine	+10 min.	-1 hour
Dunmore	+20 min.	+45 min.
Alloa	+30 min.	+1 hour
Fallin	+40 min.	+1 hour
Stirling	+1 hour	+2 hour

TRAVEL TIME BETWEEN STATIONS

Journey	Time in minutes
Stirling-Skinflats	35
Stirling-Culross	35
Skinflats-Kincardine	10
Kincardine-S.Alloa	10
S.Alloa-Fallin	5
Fallin-Stirling	15
Kincardin-Dunmore	10
Dunmore-S.Alloa	5

Table 1.2 Summary of zooplankton samples collected between December 1981 and December 1982

Date	Tide	Fallin	S.Alloa	Dunmore	Kincardine	Culross	Skinflats
11.12.81	HTS	+	+	+	+	-	-
	LTS	-	-	-	-	-	-
18.12.81	HTN	+	+	+	+	-	-
	LTN	+	+	+	+	-	-
12.1.82	HTS	+	+	+	+	-	+
	LTS	+	+	+	+	-	-
19.1.82	HTN	+	+	+	+	-	+
	LTN	+	+	+	+	-	-
27.1.82	HTS	+	+	+	+	-	+
	LTS	+	+	+	+	-	-
3.2.82	HTN	+	+	+	+	-	+
	LTN	+	+	+	+	-	-
11.3.82	HTS	+	+	+	+	+	+
	LTS	+	+	+	+	-	-
17.3.82	HTN	+	+	+	+	+	+
	LTN	+	+	+	+	-	-
26.3.82	HTS	+	+	+	+	+	+
	LTS	+	+	+	+	-	-
2.4.82	HTN	+	+	+	+	+	+
	LTN	+	+	+	+	-	-
10.5.82	HTS	+	+	+	+	+	+
	LTS	+	+	+	+	-	-
17.5.82	HTN	+	+	+	+	+	-
	LTN	+	+	+	+	-	-
24.5.82	HTS	+	+	+	+	+	+
	LTS	+	+	+	+	-	-
31.5.82	HTN	+	+	+	+	+	+
	LTN	+	+	+	+	-	-
8.7.82	HTS	+	+	+	+	-	+
6.9.82	HTS	+	+	+	+	+	+
	LTS	+	+	+	-	-	-
13.9.82	HTN	+	+	+	+	+	+
	LTN	+	+	+	+	-	-
20.9.82	HTS	-	+	+	-	+	+
	LTS	+	+	+	+	-	-
27.9.82	HTN	+	+	+	+	+	-
	LTN	+	+	+	+	-	-
3.11.82	HTS	+	+	+	+	+	-
	LTS	+	+	+	+	-	-
9.11.82	HTN	+	+	+	+	+	+
	LTN	+	+	+	+	-	-
16.11.82	HTS	-	+	+	+	+	+
	LTS	+	+	+	+	-	-
23.11.82	HTN	-	+	+	+	+	+
	LTN	-	+	+	+	-	-
15.12.82	HTS	-	+	+	+	+	+
	LTS	-	+	+	+	-	-
23.12.82	HTN	+	+	+	+	+	-
	LTN	+	+	+	+	-	-

Table 1.3 Recognition characters for stages of calanoid copepods

Appendage	Stage											
	Nauplius						Copepodite					Adult
	1	2	3	4	5	6	1	2	3	4	5	
antennule	+	+	+	+	+	+	+	+	+	+	+	+ (structure fully formed)
antenna	+	+	+	+	+	+	+	+	+	+		
mandible	+	+	+	+	+	+	+	+	+	+		
maxillule	0	0	.	-	-	-	+	+	+	+	+	
maxilla	0	0	0	0	-	-	+	+	+	+	+	
maxillipeds	0	0	0	0	0	-	+	+	+	+	+	
1st leg	0	0	0	0	0	-	+	+	+	+	+	
2nd leg	0	0	0	0	0	-	+	+	+	+	+	
3rd leg	0	0	0	0	0	0	-	+	+	+	+	
4th leg	0	0	0	0	0	0	-	-	+	+	+	
5th leg	0	0	0	0	0	0	0	-	-	+	+	
caudal rami	+	+	+	+	+	

- + relatively well developed, but not fully formed
- present as lobed structure, or otherwise undeveloped
- . present as group of setae
- 0 structure absent

between sites. Sampling on a given date commenced with either high or low tide samples depending on the times of the tides. Sampling always commenced at the seaward end of the study area.

Sampling in 1981-1982 was conducted during eight lunar cycles (Table 1.2); within each cycle, sampling commenced on a spring tide and was normally repeated at weekly intervals until the following spring tide. At each upper estuary site, a full lunar sampling cycle thus comprised a total of 8 samples. Four samples per cycle were normally taken per cycle at the lower estuary sites. On occasion, sampling was reduced to a single spring tide or a single spring-neap pair. It was not always feasible to collect all the samples scheduled for a given date. In 1983, samples were taken at the upper estuary sites only, at quarterly intervals on high spring tides. On one of these quarterly visits, a series of 8 consecutive samples was taken at Dunmore in order to evaluate small-scale temporal variability. On a separate occasion, a series of samples was taken by boat on a grid superimposed on the intertidal mudflats at Skinflats to evaluate the magnitude of small-scale spatial variability.

Sampling

A total of 248 visits to sampling stations were made, during which 528 zooplankton samples were collected.

Samples of approximately 500 l volume were taken at each site on each visit, with the sampling equipment described above. The pump was calibrated immediately before each sample; normally, the pump was operated for about 6 min. to filter the required volume.

On most occasions, there was a residual water flow at the sampling locations of at least 10-15 cm/s, and the nets were positioned down-current of the pump to ensure that previously-filtered water was not re-sampled. Sampling was conducted near the shore, in water of 50-100 cm depth. The pump head was moved slowly and continuously between the surface and about 10cm from the bottom sediment. The bottom consisted of fine mud at all sites except Culross, where sand and gravel predominated.

When no residual water movement was apparent (most frequently at Skinflats), a transect of approximately 100m was traversed slowly, with the pump head held as far in advance of any disturbance as possible (c. 2m).

Occasionally, high turbidity led to net clogging. When this occurred, the pump and stopwatch were stopped, the nets agitated gently to clear the mesh, and pumping and timing resumed. By following this procedure, it was possible to ensure that 100% of the water pumped was filtered.

Sample volumes were subsequently calculated from the recorded sample time ($\pm 0.1s$) and the calibrated pump delivery rate (volume measured $\pm 0.5 l$) for the appropriate sample.

Prior to the collection of each sample, 40% borax-buffered Steedman's solution (Steedman 1976) was made up to 4% using 20 μ -filtered ambient water. The use of local water minimised osmotic damage to the sampled organisms, which were washed gently with a minimum of filtered local water from the cod-ends of the nets into polythene jars. The contents of the 250 μ and 69 μ cod-ends were preserved separately.

In conjunction with each sample, air temperature and local weather conditions were noted; wind speed was estimated on the Beaufort scale. Two 1-litre water samples were collected in acid-washed polythene bottles. Each bottle was first filled and rinsed with local water, then squeezed flat, held 20-25 cm below the surface, and allowed to fill rapidly. Water temperature was recorded to \pm 0.5 deg.C using a direct-reading total immersion mercury thermometer. Salinity was determined to \pm 0.5 ppt using an MC5 conductivity bridge.

Estimation of small-scale temporal and spatial variability

The scales over which these sample series were taken was chosen to be relevant to the question of the confidence with which a single sample might be considered representative of local abundance; this was considered to be of the order of tens to hundreds of metres and of tens of minutes.

On 23.6.82, a series of 20 samples was taken over the intertidal region at Skinflats (Fig.1.2) to investigate spatial variation within a short time period. Sampling was conducted over a 35-minute period

from a small boat in a depth of between 1m and 2m, during slack high water on a spring tide.

The pump and nets described above were mounted on the gunwale of the boat; the nets amidships and the pump deployed laterally from the bow with the intake at a depth of about 65 cm. Boat engine speed was regulated, using a simple log and knotted line, to give a velocity of 0.5 m/s; at this speed, the pump intake was effectively free from any disturbance propagated by the boat. The net cod-ends were replaced with small polythene bottles containing 40% Steedman's solution. These bottles could be removed and replaced with fresh bottles in a few seconds, permitting samples to be taken virtually contiguously.

Samples were taken in a series of 5 parallel North-South transects (Fig.1.2), intended to provide a rectangular grid of 20 samples. Although this took place at slack high water and in the absence of wind, buoys were dropped at the beginning and end of the first and last transects to permit subsequent detection of any displacement which might have occurred. Each transect was divided into 4 60-second samples on a bearing of 0 or 180 degrees, and with a pump delivery of 76 l/min at a velocity of 0.5m/s. Samples were thus of approximately 80l volume, but the duration of sampling and thus the volume was determined independently for each sample. Cod-end bottles were changed in approximately 10s between samples, during which time the pump output was diverted away from the nets.

Temperature and salinity measurements were made at a depth of 50 cm with an MC5 temperature-conductivity bridge.

At the end of each transect the boat was turned on a course of 90 or 270 degrees for 60s before turning onto the next transect. The area

covered by the sample grid was thus approximately 120m by 120m. Pump calibration was carried out before and after sampling.

The survey site was visited approximately 18 h later at low water. The marker buoys were located and bearings taken on visible landmarks to establish their position. These bearings were transferred to an Admiralty chart in order to establish the actual shape of the sampling grid.

On 3.3.83, a series of samples was taken on a high spring tide at Dunmore. On this occasion, 8 consecutive samples were taken between high water minus 30 min. and high water plus 30 min. to investigate short-term temporal variability at a fixed point. The sampling equipment was operated and calibrated as described previously for shore-based samples. Note was taken of the direction of water movement, and the nets positioned accordingly to avoid re-sampling water.

Zooplankton sample processing

Upon return to the laboratory, zooplankton samples were rinsed in filtered seawater diluted with distilled water to the appropriate salinity, and curated in fresh Steedman's solution made up to 4‰ with water of the same salinity.

Samples frequently contained a considerable quantity of fine silt, especially in the 69 μm fraction. This was often sufficient to have interfered with subsequent counting. Where this occurred, organisms were extracted from the silt prior to final curation by a density separation technique adapted from deJorge and Bouwman(1977). This method involves the use of a colloidal silica, Ludox TM, which has density of 1.3 g/cc.

The sample was concentrated to a volume of 50 ml and added to 100ml of 50% Ludox(diluted with distilled water). The mixture was stirred thoroughly with a glass rod, a magnetic follower added, and a 1 cm deep layer of distilled water floated on the surface of the mixture. The addition of distilled water prevented dessication of the Ludox, which causes a change of state from liquid to gel. The mixture was placed on a magnetic stirrer, and the speed adjusted until sediment was re-suspended to about half the depth of the vessel. Stirring continued for one hour, after which organisms were gently aspirated from the Ludox-distilled water interface into a 1-litre Buchner flask containing fresh 4‰ Steedman's solution. A fresh layer of distilled water was floated on the surface of the Ludox and a

second extraction performed.

This method of extraction proved to be effective in separating all soft-bodied organisms, as well as foraminifera, small bivalve larvae and juvenile gastropods (principally Hydrobia). Attempts to assess the effectiveness of the method for soft-bodied organisms revealed that an exhaustive examination of the remaining sediment was required to detect the few remaining individuals. deJorge and Bouwman (1977) reported that formalin preservation appeared to prevent adherence of specimens to silt particles; this proved to be the case in the present study.

Following Ludox separation the remaining silt was scanned rapidly at low magnification to detect any larger, denser organisms, which were removed and added to those already separated.

All zooplankton counts were performed using either a Bausch and Lomb or Wild M5A dissection microscope, the latter equipped with light and dark field illumination. Subsamples or aliquots were placed in a modified Bogarov tray with a volume of 2ml. Where practicable, successive aliquots were counted until the entire sample had been examined. This minimised abundance estimation error and ensured that relatively rare taxa were registered.

Where total numbers were sufficiently large to make subsampling necessary, the sample was diluted to an appropriate volume (determined from a preliminary count), agitated thoroughly, and subsampled with a 2ml Stempel pipette. Successive subsamples were withdrawn (without replacement) until at least 100 of the more abundant categories had been counted (Frolander, 1968), following which the entire sample was scanned with the aid of a fine dissecting needle for less abundant taxa.

Identification of taxa followed the authorities below:

ICES Zooplankton sheets

Acartia
Centropages
Chaetognatha
Polychaete larvae
Rotifera
Appendicularia

Sars, G O (1895-1928)
An account of the Crustacea
of Norway

Copepoda

Rose, M 1933
Copepodes Pelagiques
Faune Fr. 26 Paris

Copepoda

Hartmann-Schroder 1971
Die Tierwelt Deutschlands
Annelida 58 Teil

Polychaeta
(esp. Maranzelleria)

Newell G E and Newell R C 1977
Marine Plankton, Hutchinson

Additional information on a
variety of taxa

Formal identification was accomplished by dissecting (where appropriate) organisms in lactic acid, mounting the diagnostic structures in polyvinyl lactophenol, and examining at 400x under a compound microscope.

The commoner copepods were identified to species, and, where practicable, recorded as adult, copepodite or nauplius. A large category of copepod nauplii remained unassigned to species, however.

All developmental stages of Eurytemora affinis were enumerated separately, using Table 1.3 and descriptions in Katona (1971). For 9 sampling dates (Table 1.7) the mean length of up to 50 preserved specimens of each stage was determined using a calibrated eyepiece graticule. Nauplii were measured at 200x, to the nearest 10 μm , while copepodites and adults were measured at 120x to the nearest 16.6 μm . For the purposes of examining the size-frequency distribution of adults, copepods were grouped into 0.02mm size classes. Male and female copepodites of stages 4, 5 and 6 were counted and measured as separate groups.

The length of nauplii was measured excluding the caudal armature. Copepodite length was measured as the length of the cephalothorax, excluding the 'wings' on the final thoracic segment in the case of stage 5 and 6 females.

On 27.4.82, samples were taken to determine the effect of preservation on adult body length. Copepods were first killed or rendered comatose by raising the water temperature to 30deg.C over a period of 30 min. 100 adult females were randomly removed from the sample and their cephalothorax lengths measured as described above. They were then transferred to 4% Steedman's solution and stored for two weeks. Water collected at the time of capture and 1.2 μm -filtered was used throughout, to minimise osmotic changes which might have affected body dimensions. The sample of 100 copepods was re-measured after two weeks and the mean pre- and post-preservation lengths compared by t-test.

Numerical analysis of zooplankton survey data

The frequency of occurrence of taxa in all samples and by sample category was computed. Samples were classified by logical category (high/low, spring/neap, by station, etc.), and a chi-squared test of association between frequency of occurrence and logical category carried out.

Multivariate analyses

The survey data were analysed by logical category using classification and ordination techniques. The primary methods were routines in the Cornell Ecology Series of programs: Twinspan (classification: Two-Way Indicator Species Analysis, Hill 1973) and Decorana (ordination: DETrended CORrespondence ANALysis, Hill 1979).

Twinspan (TS) is a polythetic divisive method of classification. For purposes of comparison, a synthetic agglomerative method was also tested; for each sample category a similarity matrix was generated using the Bray-Curtis index (log $x+1$ transformed data) and a dendrogram constructed by group-average sorting (CLUSTAN, Wishart 1970).

All TS and Decorana (DCA) analyses were conducted on data subjected to quasi-logarithmic transformation; abundance classes of 0-30, 31-100, 101-1000, 1001-10000, 10001-100000 and >100000 were used. These intervals were used as the cut levels for defining TS pseudospecies; in effect, and for the purposes of computation, each abundance class is regarded as a 'species', although indicator species are still defined by their presence or

absence. An upper bound of 30 was used for the smallest abundance class to avoid undue influence from taxa occurring in low numbers. Cassie (1962) amongst others has reported a high degree of uncertainty in estimating population abundance when the number of individuals in a sample is small, and it was considered that abundances between 10 and 30 per cubic metre could not be reliably distinguished.

In both TS and DCA analyses, the supplied option to downweight rare species was invoked.

For the purposes of TS classification, samples and taxa were each assigned 8-character identifiers. For samples, the identifiers were constructed as follows:

Character	Purpose
1	Letter identifying station (F,S,D,K,G,C)
2-6	Digits identifying date
7-8	Letter identifying tidal state (HS,LS,HN,LN)

Taxa were allocated 4 characters for generic name and four characters for specific name, e.g. ACAR LONG represents Acartia longiremis. Where taxa were not identified to species, a suitably obvious alternative was used, e.g. rotifers were identified as ROTI SPEC.

A suite of Fortran programs was developed to re-format data structures for the various analyses, produce raw data tabulation and generate similarity matrices (Roddie 1986).

Subdivision of the entire data set into logical categories permitted the removal in turn of seasonal, spatial and temporal effects on community structure.

Relationships between community structure and environmental, spatial and temporal variables.

a) DCA

For each analysis, the first two DCA axes were plotted, and Spearman rank correlation coefficients between major variables and the sample scores on these axes computed.

b) TS

For each analysis, a TS two-way ordered table and a sample dendrogram were produced.

Multiple Discriminant Analysis (MDA, = canonical variate analysis) was used to relate environmental variables to classification group membership (Green and Vascotto 1978, Wright et al 1984, Furse et al 1984).

Following the recommendations of Green and Vascotto (1978), all variables (log x+1 transformed) were entered simultaneously into the analyses, which were implemented by an SPSSx routine (Nie 1975). MDA uses the grouping assigned to samples by a previous classification (in this case on the basis of sample taxonomic composition) and derives a linear combination of variables which maximises the ratio of between-group to within-group variance. Only those variables which had a significant univariate F-ratio ($p < 0.05$) for a particular sample category were used in the analysis for that category.

Following derivation of the rule, the samples are re-classified and the percentage successful re-classification calculated. Discriminant factors are derived which permit the samples to be located in 2-dimensional discriminant space and enable a visual assessment of the power of the analysis in discriminating group structure on the basis of related variables.

A convenient method of displaying the influence and relative importance of variables is to plot the classification group centroids in multiple discriminant space, and to project onto the plot vectors which indicate the direction and relative magnitude of influence of the variables in discriminating between groups (Overall and Klett, 1972). All vectors originate at the overall sample group centroid in discriminant space; their endpoints are defined by co-ordinates which, for each axis, are the products of the univariate F-ratio (between- to within-group variance ratio) for a variable and the correlation between group variable mean and group discriminant function score mean. Thus, the direction of the vector is a function of the degree of association between each discriminant function and a variable, and the length of the vector a reflection of the degree to which a variable is related to group structure.

Water samples

Prior to 3.2.82, only salinity and temperature were measured, using an MC5 temperature-conductivity bridge calibrated at regular intervals against a silver nitrate titration. Salinity was recorded to 0.1 ppt, and temperature to 0.5 deg.C. From 13.2.82, measurements were made of suspended solids, chlorophyll a and chlorophyll breakdown products (phaeopigments). All determinations were made following the methods of Strickland and Parsons(1968).

Suspended solids were measured by filtering 250-1000 ml of sample water onto pre-ashed, tared (+/- 0.01 mg), Whatman GF/C glass-fibre filters with a nominal retention of 1.2 um. At least two 1.2 um-filtered seawater blanks of comparable volume were carried through in conjunction with each set of samples. A single sample only was processed in association with each zooplankton sample. After filtration of each sample the filter was rinsed three times with 10 ml distilled water to remove salts, placed on clean aluminium foil and dried at 60 deg.C for at least 12 h. Dried filters were cooled in a dessicator for 1h, weighed to the nearest 0.01 mg, placed on clean aluminium foil, and ashed for 2 h at 450 deg.C. Filters were again cooled in a dessicator before re-weighing. Dry and ash weights were corrected for average blank changes, and the results expressed as corrected dry and ash-free dry weight.

Analysis for chlorophyll a and phaeopigments was carried out on 200ml samples filtered onto Whatman GF/C filters. Filters, with retained material, were folded twice and placed in polythene centrifuge tubes containing 12 ml 95% acetone (made up with Analar acetone and distilled water, and neutralised with sodium bicarbonate). Centrifuge tubes were

incubated overnight in a darkened refrigerator at 7 deg.C to allow extraction of photosynthetic pigments to take place. After at least 18h extraction, the tube contents were centrifuged at 3000 rpm for 10 minutes. The supernatant was decanted into a quartz spectrophotometer cuvette with a 10 cm path length.

Optical density was measured on a Cecil UV spectrophotometer against a 95% acetone blank at 663 nm and 750nm. The latter wavelength was used to correct for general sample turbidity; no known photosynthetic pigments absorb at this wavelength. Following initial measurement, the sample and blank cells contents were acidified by the addition of 5 drops of 10% HCl and allowed to stand for 5 min. to allow any transient turbidity to clear. Optical density was re-measured at the same wavelengths as before. Chlorophyll a concentration, phaeopigment concentration, and the acid ratio (a measure of the health of the phytoplankton population) were calculated using the equations of Strickland and Parsons (1972).

Results of field survey

Environmental variables

Seasonal variation in measured environmental variables will be examined on a station-by-station basis. The variables considered are:

salinity

temperature

chlorophyll a

phaeopigments

total and organic suspended solids

Additionally, for the purposes of investigating influences on zooplankton community structure, tidal state, time, and freshwater discharge to the upper estuary will in a subsequent section be treated as environmental variables.

All observations on measured variables are tabulated by station and tide in Appendix A.

Temperature and salinity

Fallin

Low tide salinity at Fallin ranged from 0‰ to 0.8‰, whilst high tide salinity encompassed a range of 0‰ to 12.2‰ (Table A1 ,Fig.1.3a). On only two occasions did salinity exceed 5.7‰.

Temperature varied annually between 0 and 19 deg.C, following an approximately symmetrical curve (Table A1, Fig.1.3b). High and low tide temperatures corresponded closely throughout the year. A temperature range of up to 6 deg.C during a single sampling cycle (11-17 deg.C, May-June 1982) was observed.

S.Alloa

There was a wide discrepancy between the high and low tide salinity curves at S.Alloa (Table A2, Fig.1.3c). The difference being most pronounced in summer and least pronounced in autumn and late winter/spring. Low tide salinity range was 0-5.5‰, and high tide salinity range was 2.0-22.6‰. Low tide salinity varied little within any sampling cycle, but high tide salinity displayed a wide range (up to 13.9 ‰) within sampling cycles.

Temperature displayed a closely similar range and pattern to that at Fallin (Table A2, Fig.1.3d).

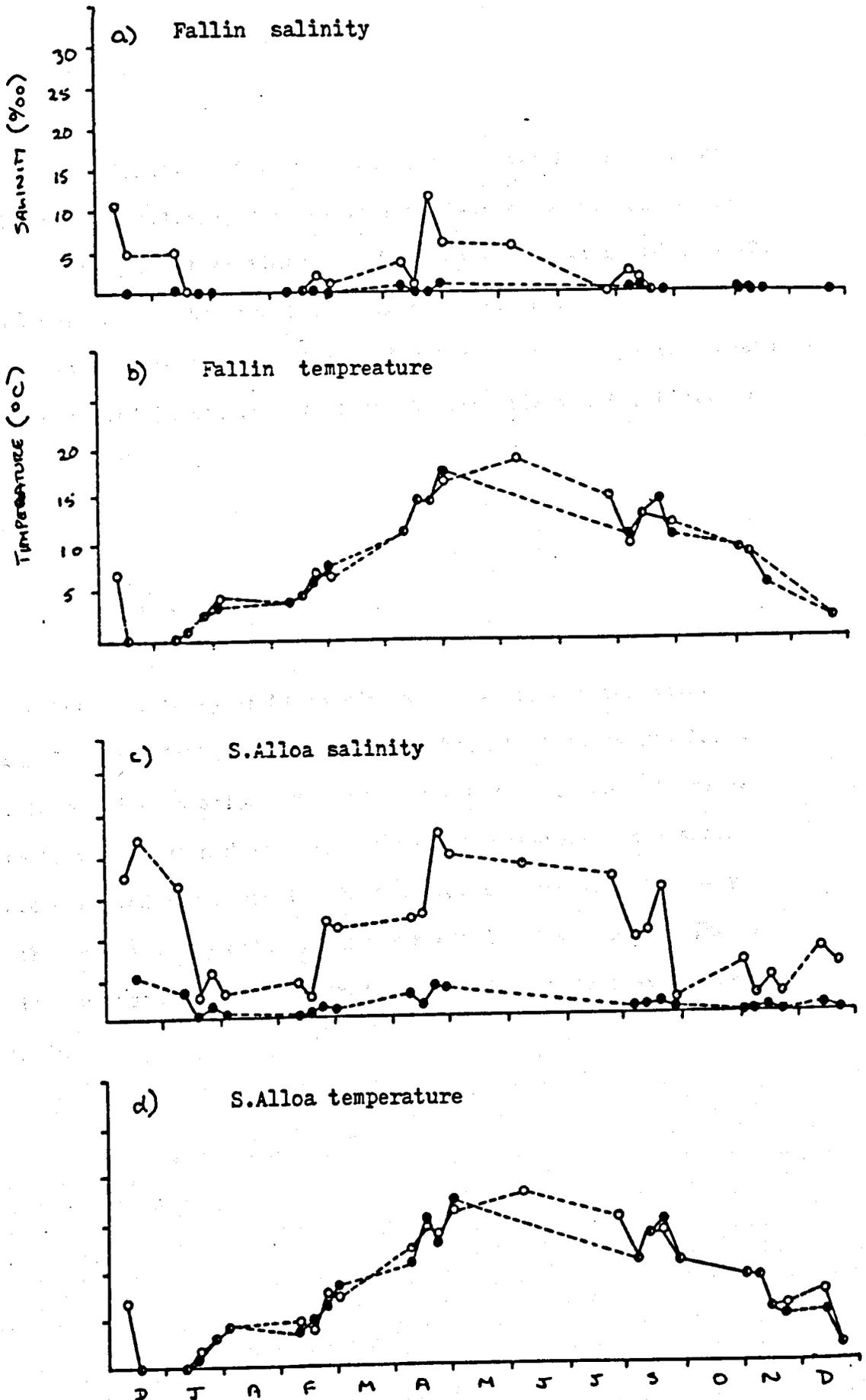


Figure 1.3 Annual variation in salinity and temperature at Fallin (a,b) and S.Alloa (c,d). Open symbols = high tide
Closed symbols = low tide

Dunmore

The pattern of salinity variation at Dunmore was similar to that at S.Alloa (Table A3, Fig.1.4a), with maximum salinities occurring in the summer and during equinoctial tides. Low tide range was wider (0.6-14.0‰) than at S.Alloa, as was the high tide range(3.8-28.5‰).

Temperature ranged between 0 deg.C and 17.0 deg.C, and the pattern again matched that observed in stations further up-estuary(Table A3, Fig.1.4b).

Kincardine

Minimum low tide salinity at Kincardine was 3.4 ‰, and the maximum observed was 23.0 ‰ (Table A4, Fig.1.4c). The high tide range was 10.4‰ to 31.5‰. Compared to stations further up the estuary, the difference on any date between high and low tide salinities was relatively small.

Temperature occupied the range 1.5-16.5 deg.C, and was thus slightly reduced with respect to up-estuary stations (Table A4, Fig.1.4d). The annual pattern of variation in temperature was similar to that at up-estuary stations.

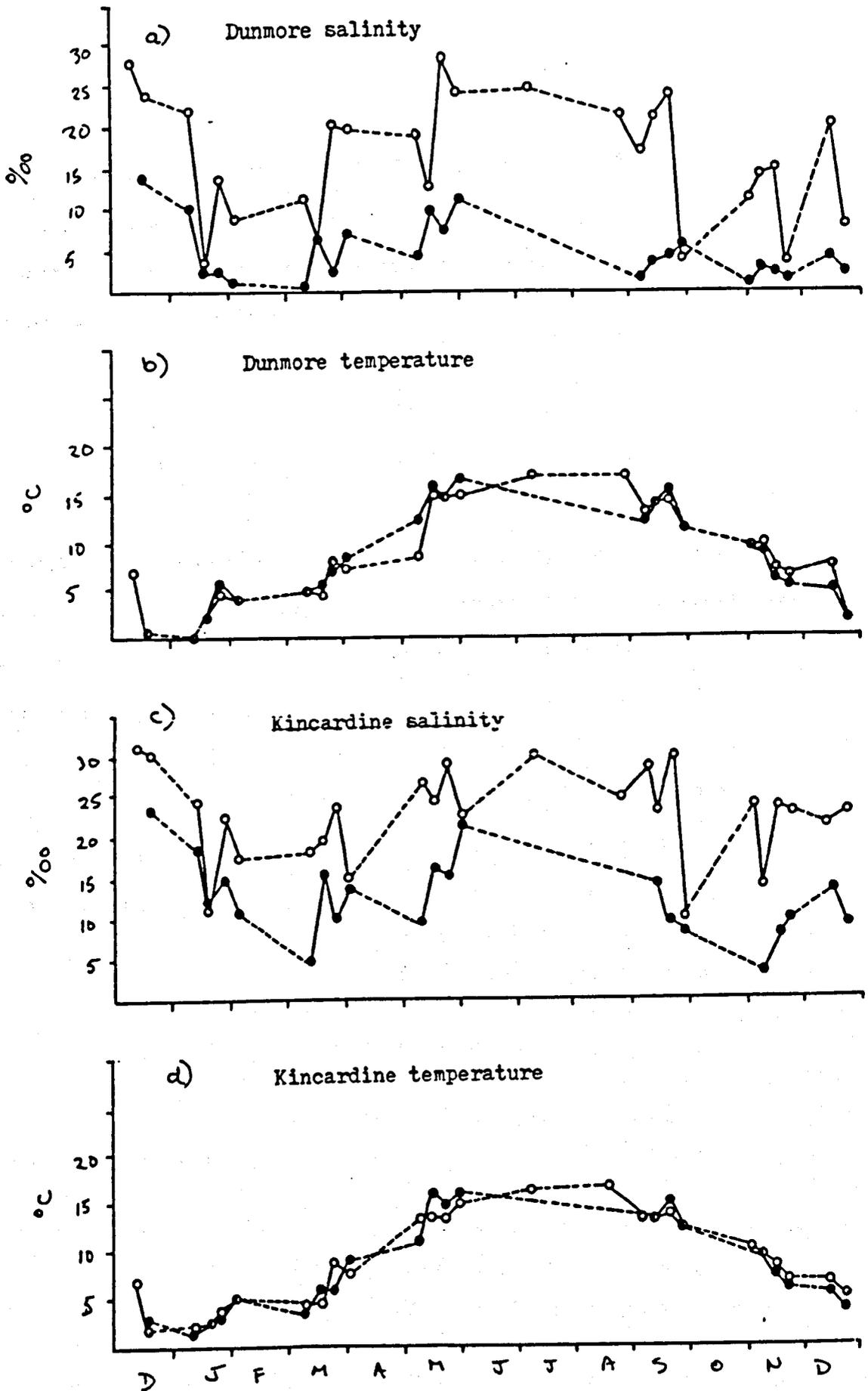


Figure 1.4 Annual variation in salinity and temperature at Dunmore (a,b) and Kincardine(c,d). Open symbols = high tide
Closed symbols = low tide

Skinflats

Salinity varied between a maximum of 31.0‰ and a minimum of 15.8‰ (Table A5, Fig. 1.5c), and temperature between 0 and 21.0 deg.C (Fig. 1.5d). Neither the pattern of salinity variation nor that of temperature corresponded closely to those at other stations.

Culross

Salinity at Culross varies relatively little throughout the year, showing only one major reduction (to 10.6‰) in late September (Table A6, Fig. 1.5a). Salinity was normally in excess of 20‰, and reached a maximum of 32.6‰. The reduction in salinity in late September closely matched similarly abrupt reductions at Kincardine, Dunmore, and S. Alloa.

Temperature ranged from 5.5 deg.C to 27.5 deg.C; both minimum and maximum values were higher than those of other stations, but the seasonal pattern was otherwise similar.

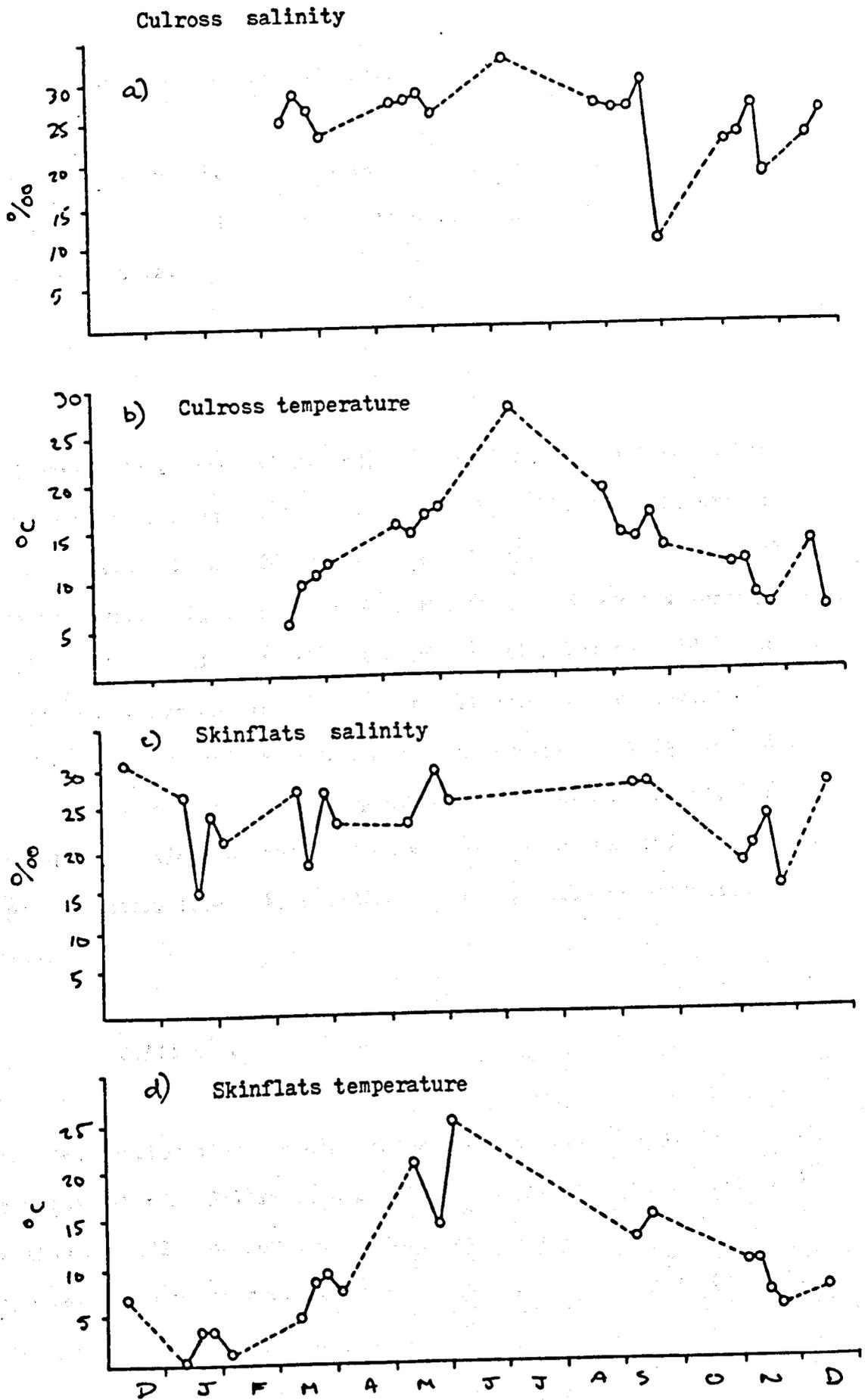


Figure 1.5 Annual variation in salinity and temperature at Culcross (a,b) and Skinflats(c,d). High tide samples only.

Suspended solids and photosynthetic pigments

These variables will not be reported in detail here; the data will be analysed more comprehensively in conjunction with the analysis of zooplankton survey data.

Fallin

Suspended particulate material exceeded 200 mg/l on 3 occasions on high tide, but on 5 occasions on low tides (Fig.1.6a,b; Table A1). The organic proportion lay between 10 and 20% for both tidal states. On low tides, there was a tendency towards higher suspended particulate loads on low spring tides.

Chlorophyll a and phaeopigments showed less variation between tidal states; the latter pigment class consists of chlorophyll breakdown products and predominated over chlorophyll a on all occasions except one (Fig.1.6 c,d).

The acid ratio, an indicator of phytoplankton health (1= senescent, 1.7= healthy) reached a maximum on the same date, but did not otherwise exceed 1.52 and predominantly took values indicating a low ratio of production to breakdown.

S.Alloa

Both suspended particulates and pigments at S.Alloa showed less variability and lower values than at Fallin on high tides, but greater variability and magnitude than at Fallin on low tides (Table A2, Fig.1.7).

Acid ratio reached a maximum of 1.67 on the same date in July as the Fallin

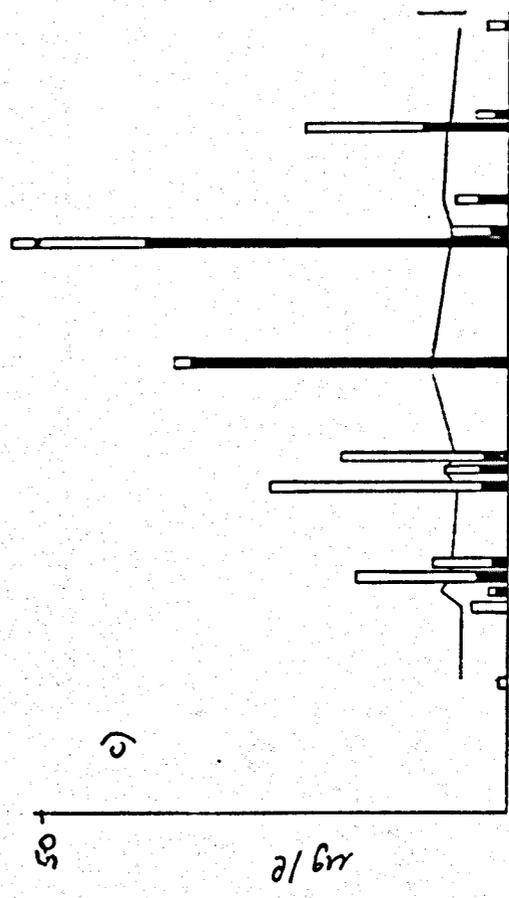
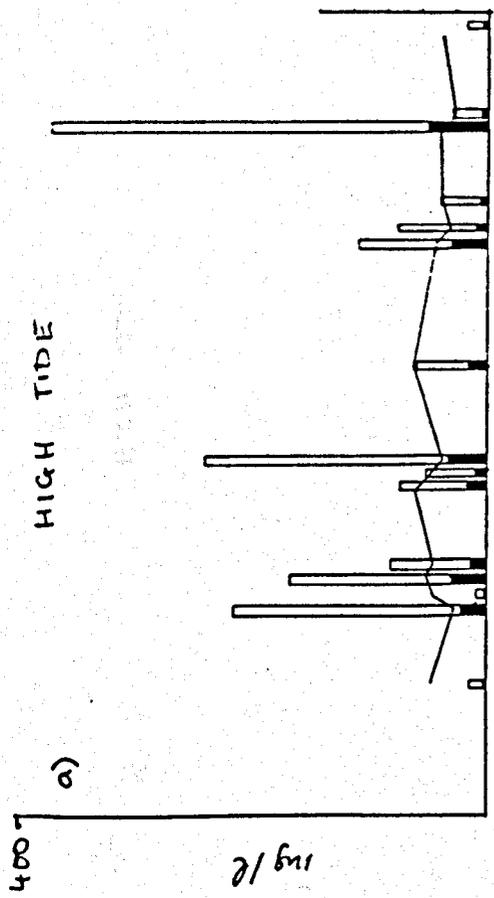
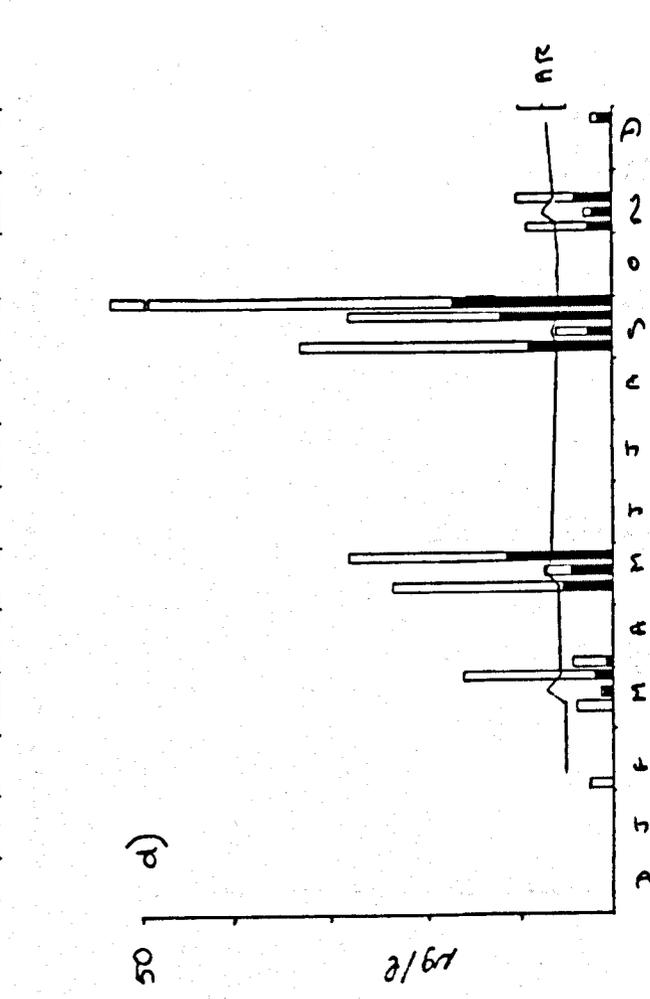
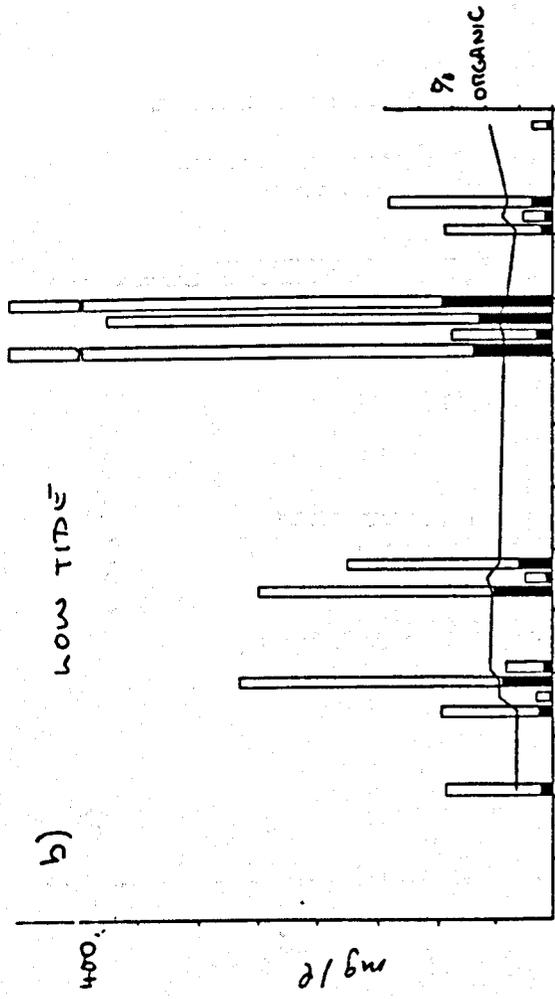


Figure 1.6 Annual variation in total suspended solids (% organic shaded)(a,b) and total pigments (chl a shaded)(c,d) at Fallin. Percent organic plotted as trend in a,b; acid ratio plotted as trend in c,d.

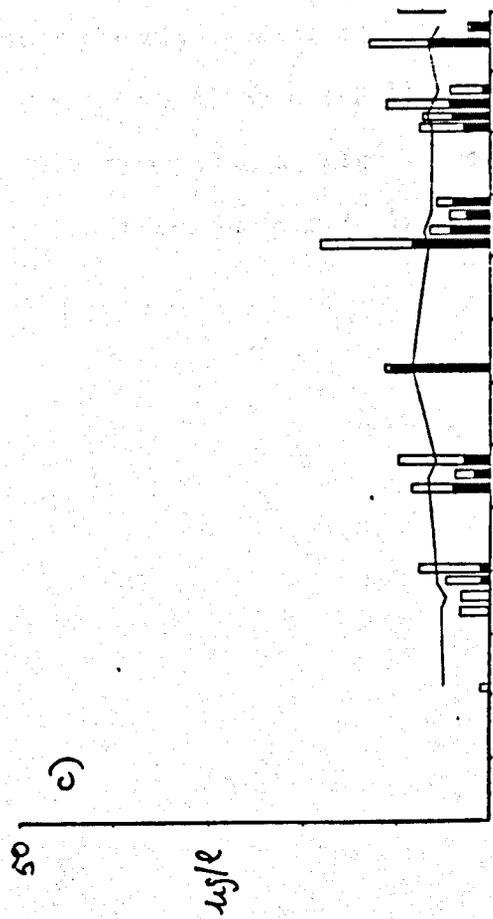
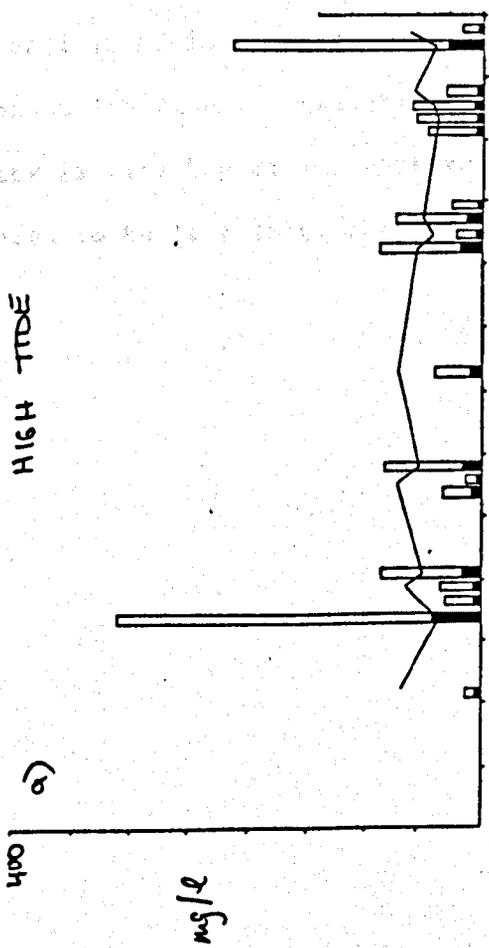
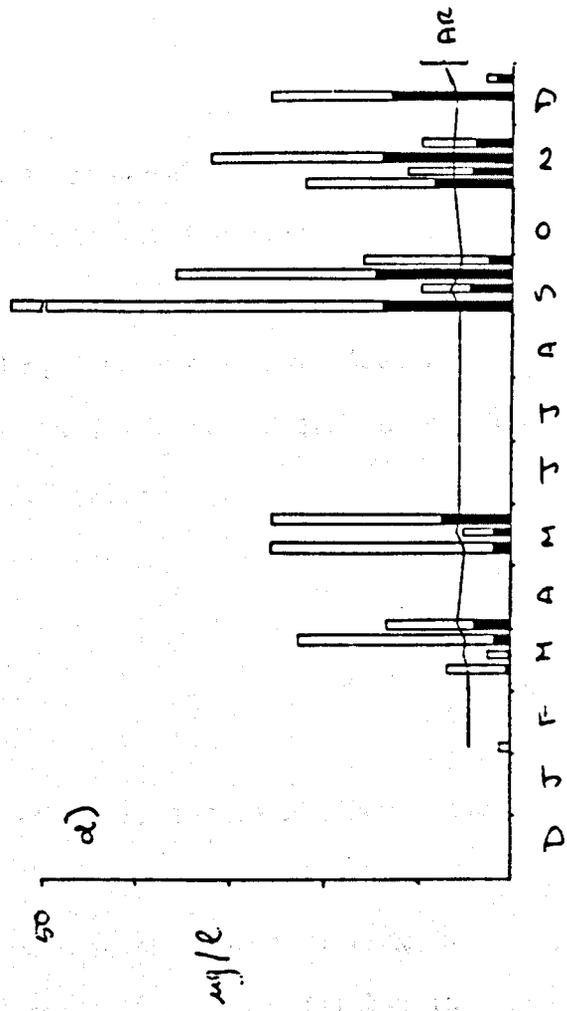
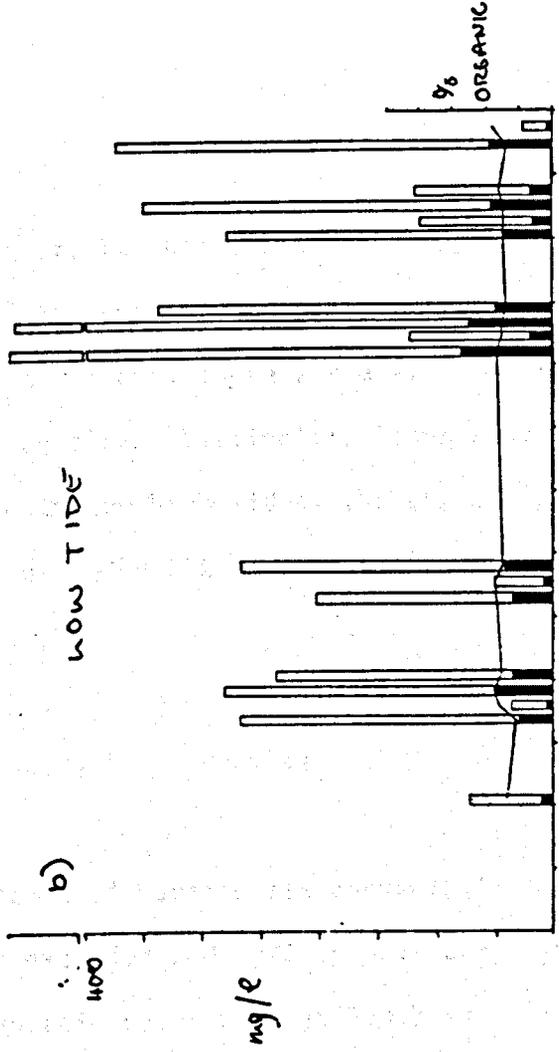


Figure 1.7 Annual variation in total suspended solids (% organic shaded)(a,b) and total pigments (chl a shaded)(c,d) at S.Alloa. Percent organic plotted as trend in a,b; acid ratio plotted as trend in c,d.

maximum, but otherwise generally indicated a preponderance of breakdown products over viable photosynthetic products (Table A2, Fig.1.7).

On low tides, there was a tendency towards higher particulate loads on spring tides. Particulate loads exceeded 200 mg/l on eleven low tides but on only two high tides. The organic percentage did not exceed 18% on low tides but exceeded 25% on four high tides (Table A2, Fig.1.7).

Dunmore

Suspended particulate concentrations exceeded 200 mg/l on eight low tides, but exceeded 100 mg/l on only one high tide (Table A3, Fig.1.8); this high tide value was, at 853.3 mg/l, the highest value recorded during the survey. The organic content of the suspended particulate material lay in the range 13-22% for low tides but was 13-31% on high tides (Fig.1.8).

The seasonal trend in primary production was more clearly evident on high tides than on low tides, a feature also of the data for S.Alloa and Fallin. Pigment levels were higher and more variable on low tides than on high tides and appeared to be to a large degree associated with suspended particulate levels.

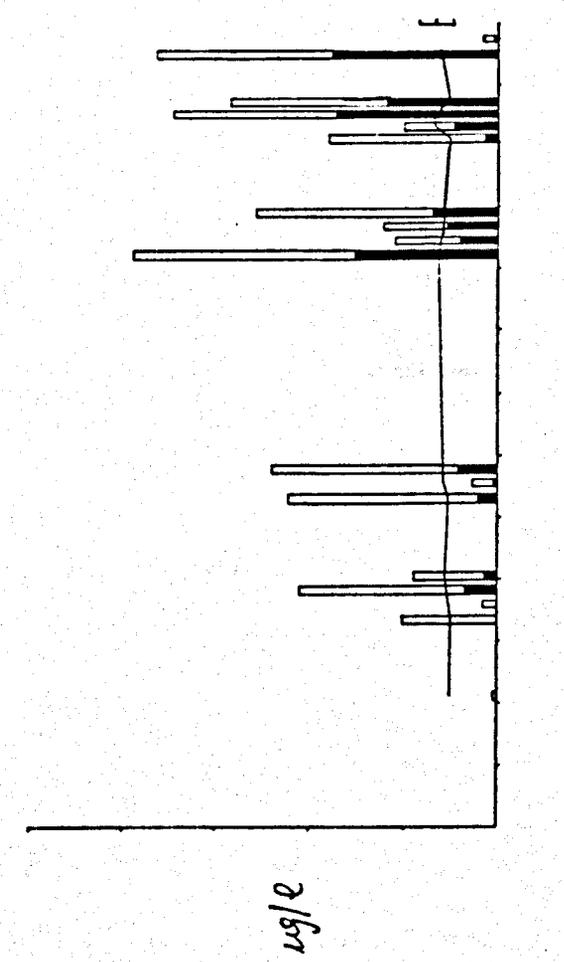
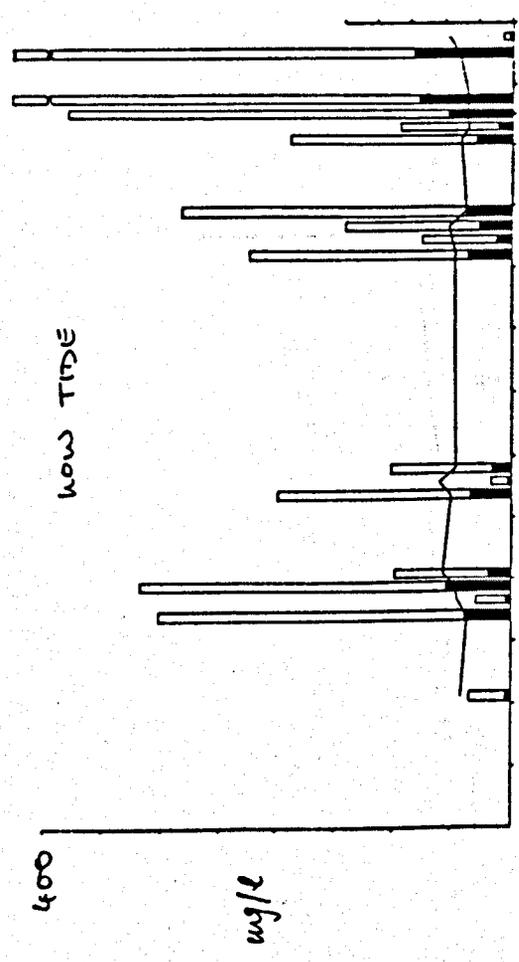
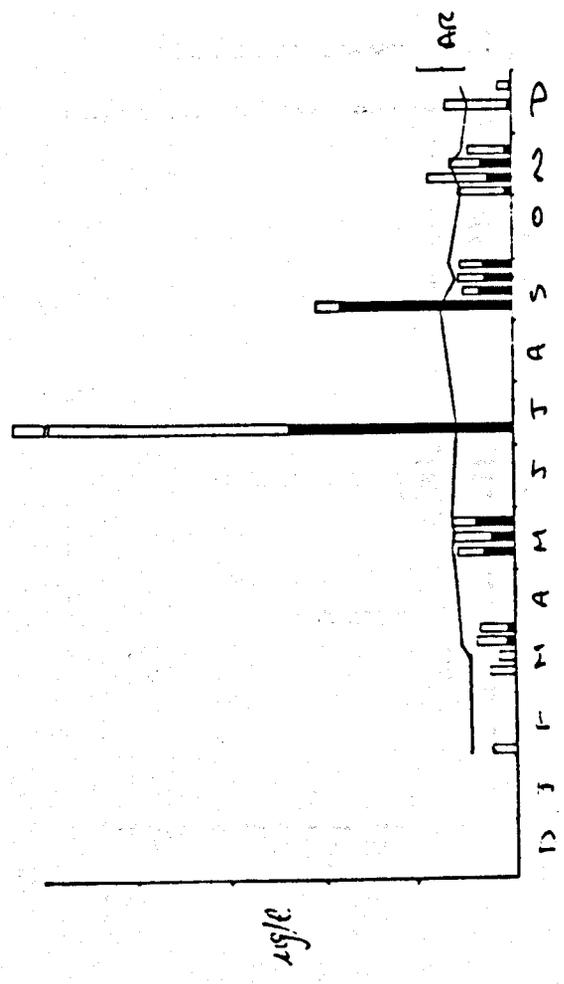
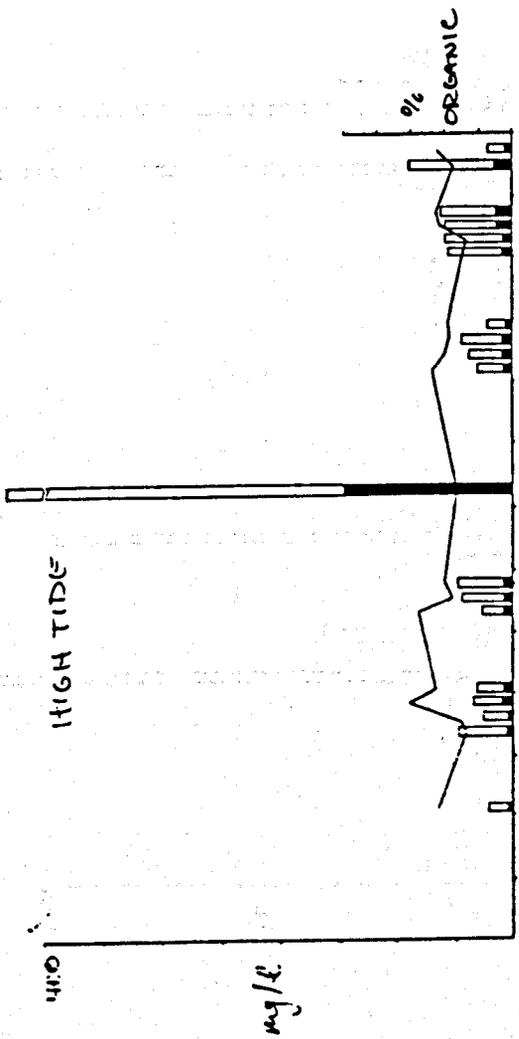


Figure 1.8 Annual variation in total suspended solids (% organic shaded)(a,b) and total pigments (chl a shaded)(c,d) at Dunmore. Percent organic plotted as trend in a,b; acid ratio plotted as trend in c,d.

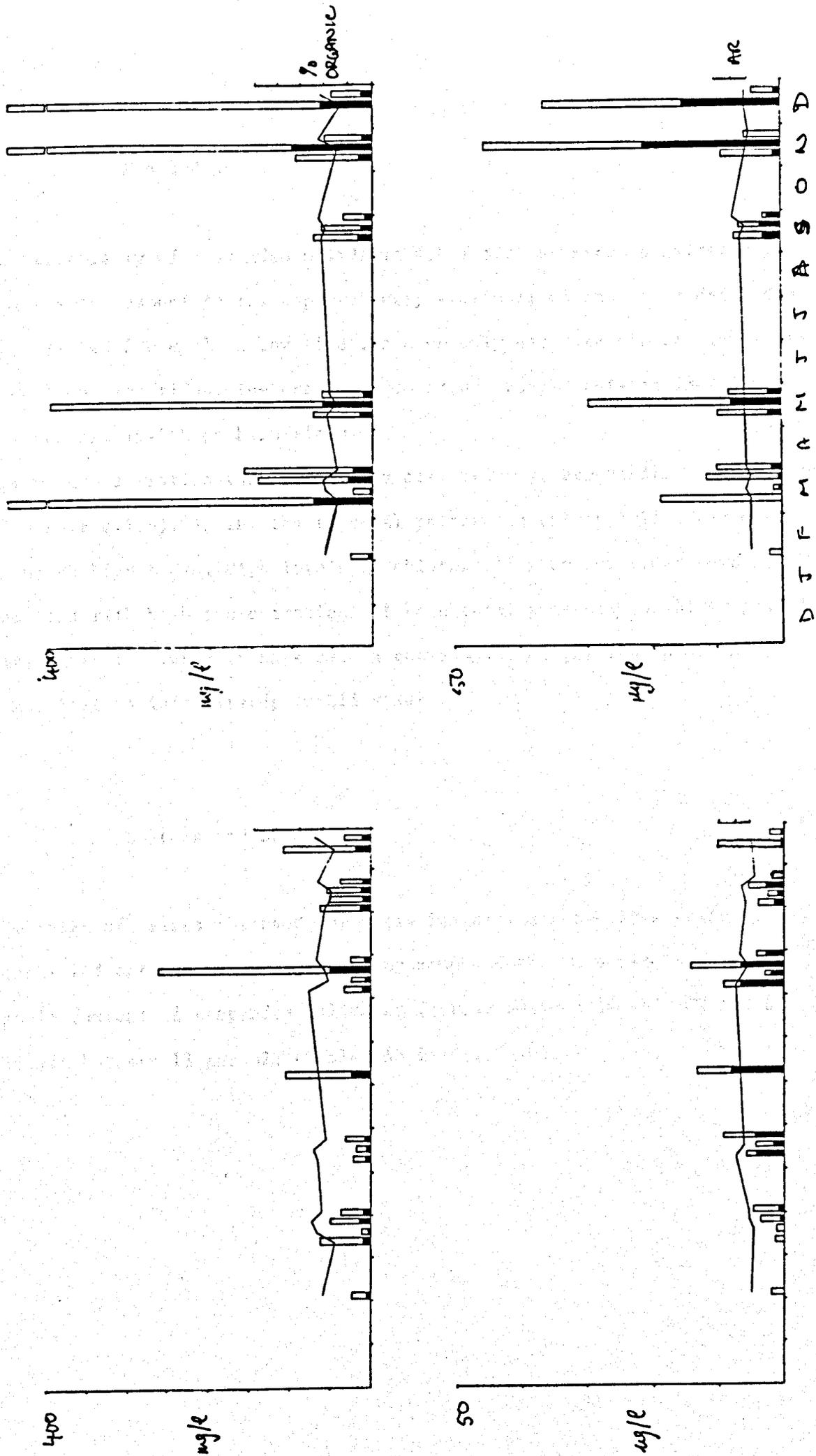


Figure 1.9 Annual variation in total suspended solids (% organic shaded)(a,b) and total pigments (chl a shaded)(c,d) at Kincardine. Percent organic plotted as trend in a,b; acid ratio plotted as trend in c,d.

Kincardine

The variability of suspended solids at Kincardine appeared considerably reduced with respect to the upper-estuary stations; on only four dates did levels exceed 200 mg/l on low tides, and on only one date did levels exceed 100 mg/l on high tides. The organic proportion ranged between 13-22% on low tides and 15-26% on high tides.

Pigment concentration variability was also reduced, especially on high tides (Table A4, Fig. 1.9). Again, the seasonal pattern in chlorophyll a was most evident on high tides. High levels of chlorophyll a on low tides were associated with high concentrations of both total pigments and of suspended solids; this is likely to have been a consequence of the resuspension of benthic diatoms into already-turbid water.

Culross and Skinflats

The range of values observed for variables at these two lower-estuary stations indicated considerable damping compared to the upper estuary.

Organic content of suspended solids at Culross between 14 and 30% and at Skinflats between 13 and 32% (Tables A5,6; Fig. 1.10).

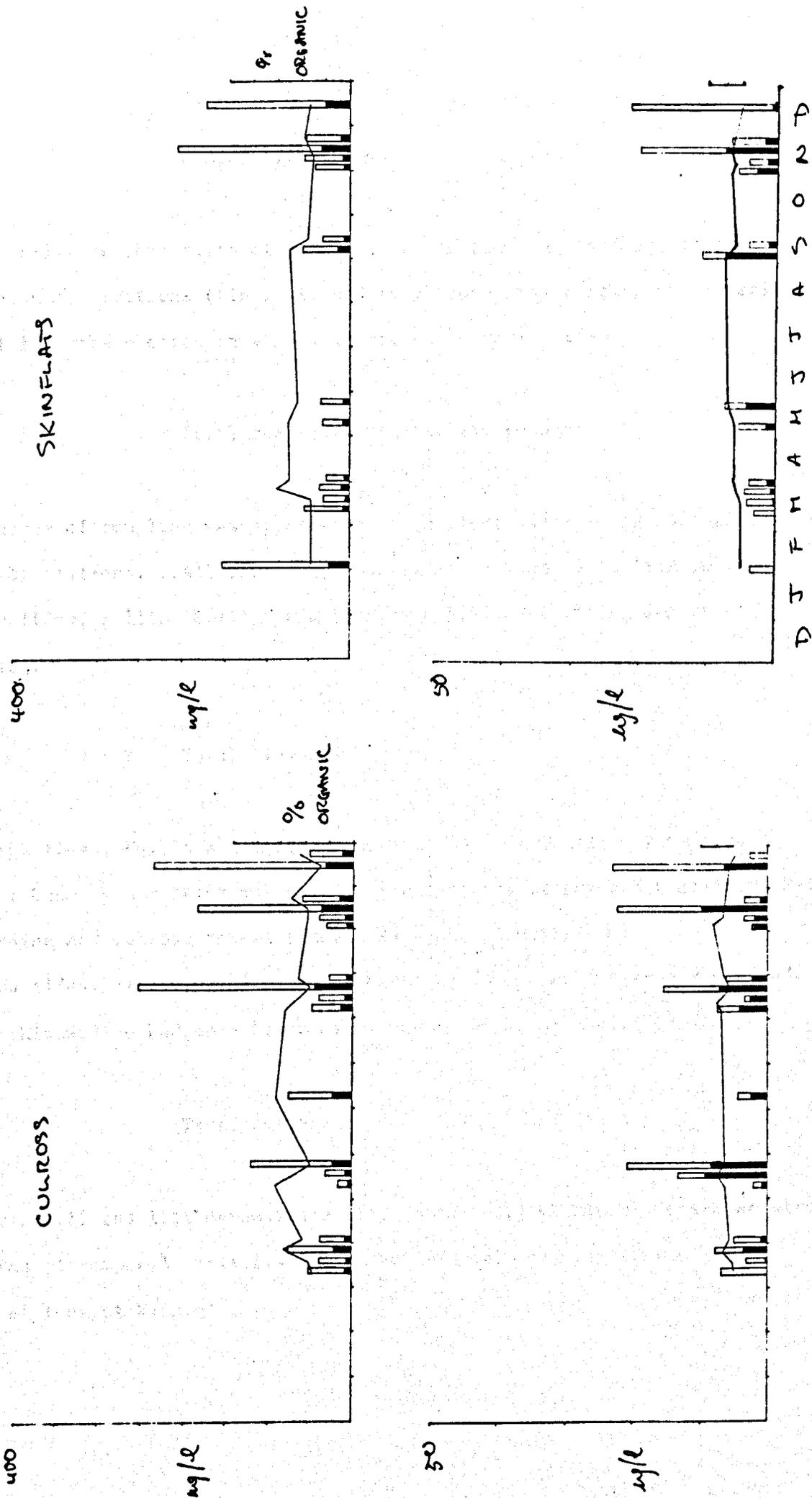


Figure 1.10 Annual variation in total suspended solids (% organic shaded) and total pigments (chl a shaded) at Culross (a,c) and Skinflats (b,d) Percent organic plotted as trend in a,b; acid ratio plotted as trend in c,d.

Comparative trends

To facilitate comparison of seasonal trends between stations, total pigment concentrations (Fig.1.11) and total suspended particulate material (Fig.1.12) were plotted on a logarithmic scale versus time.

Total suspended particulate material

A degree of coupling was apparent on high tides between the following pairs of stations: S.Alloa/Fallin, Dunmore/Kincardine, Skinflats/Culross. On low tides, Fallin, S.Alloa and Dunmore exhibited a strong degree of coupling.

Total Pigments

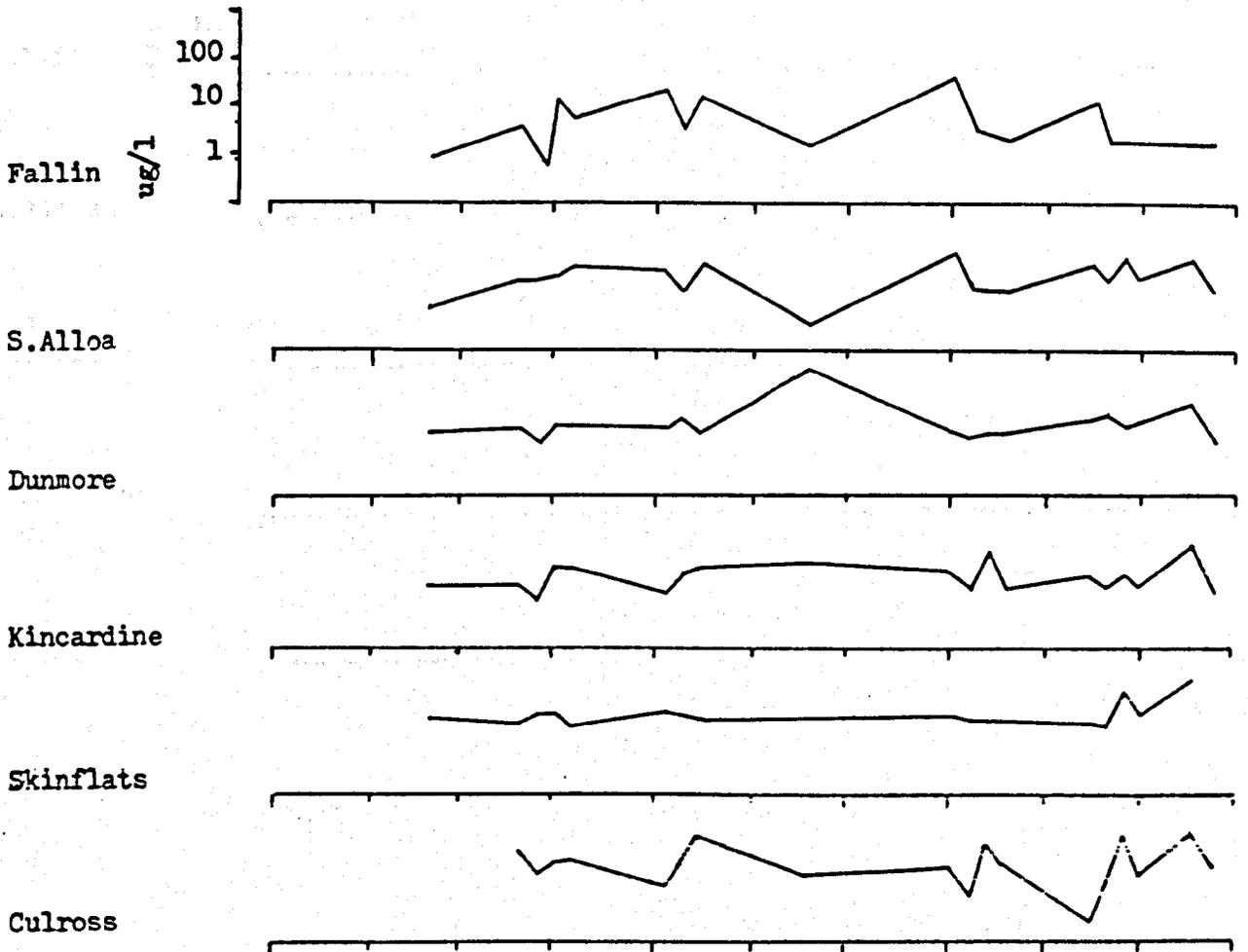
On high tides, Fallin and S.Alloa appeared to be coupled to some extent. Neither Dunmore nor Skinflats matched the patterns at any other stations, but Kincardine and Culross showed similar patterns of variation.

On low tides, Fallin, S.Alloa and Dunmore again appeared strongly coupled, whilst Kincardine had some features in common with these stations.

Trend Summary

Figures 1.11 and 1.12 demonstrate that, especially within the upper estuary, patterns of temporal variation environmental variables may extend over a scale of tens of kilometres.

Total Pigments - High Tide



Total Pigments - Low Tide

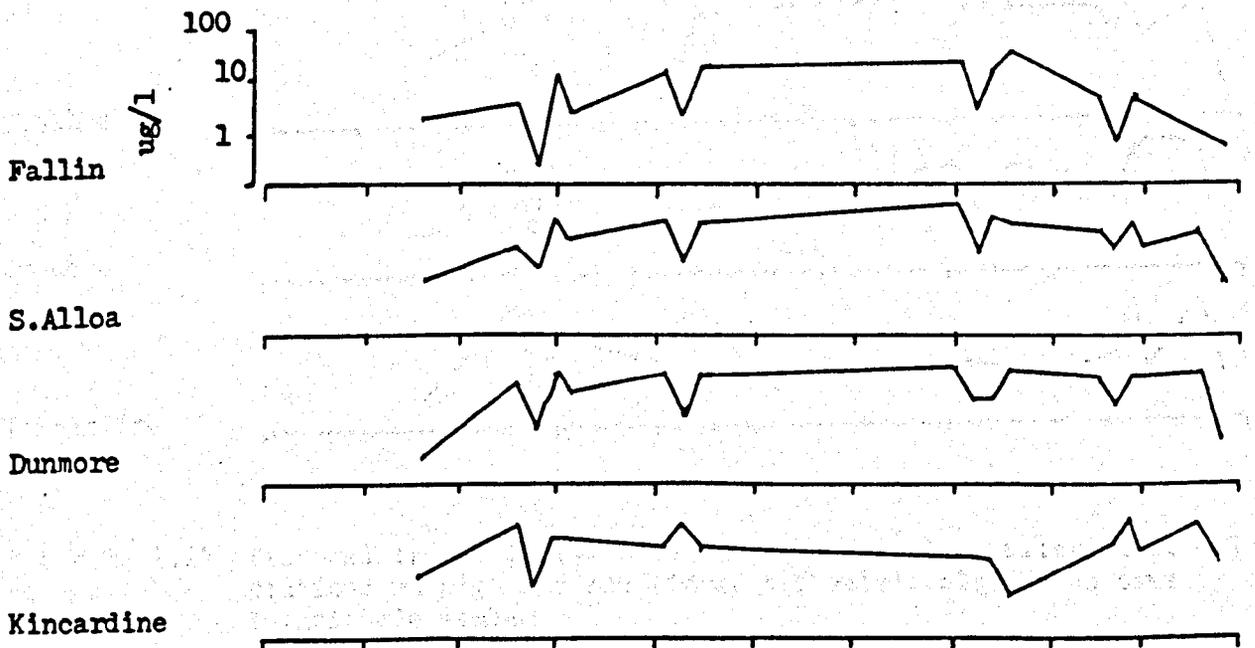


Figure 1.11 Seasonal trends in total photosynthetic pigments at all stations on high and low tides. All values plotted on same logarithmic scale

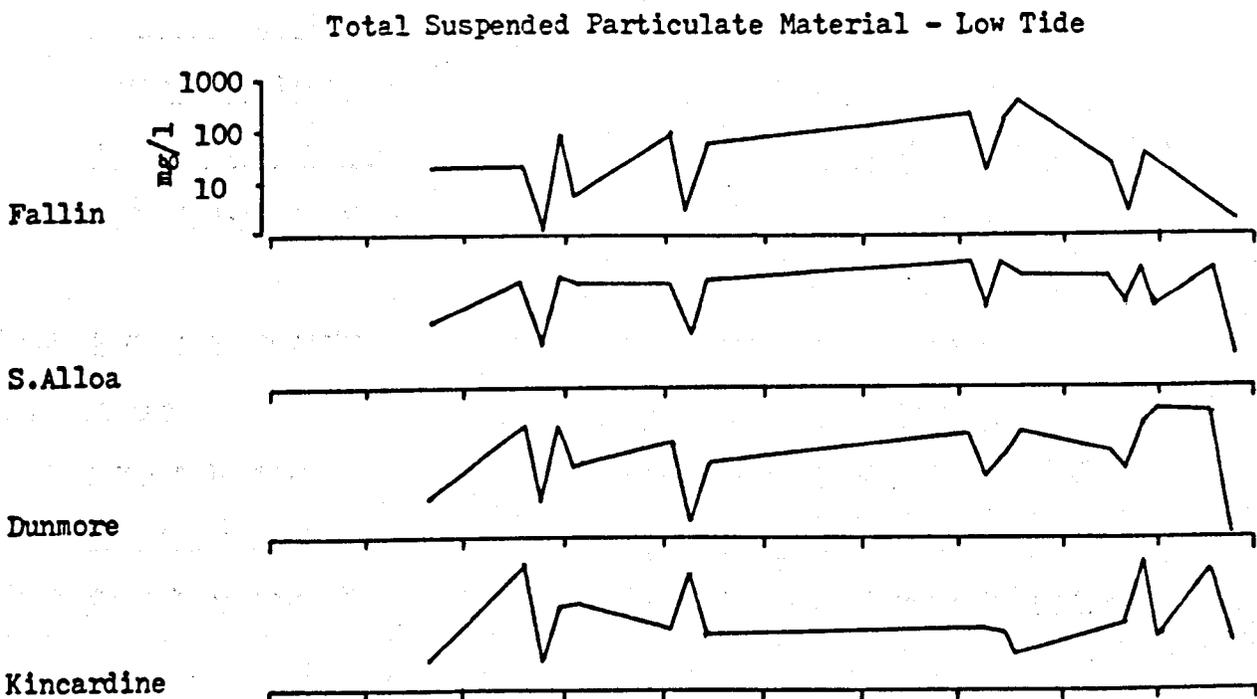
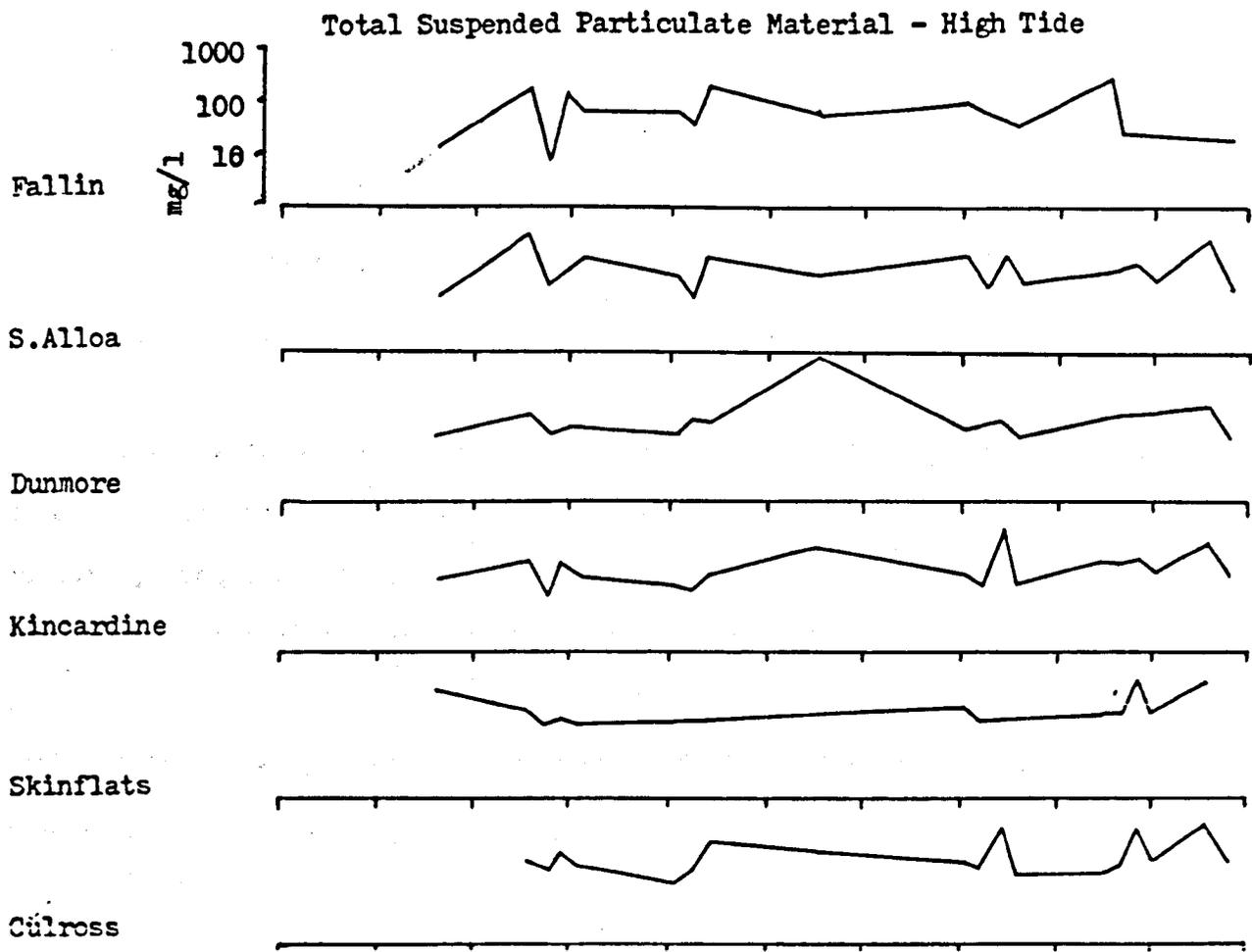


Figure 1.12 Seasonal trends in total suspended particulate material at all stations on high and low tides. All values plotted on same logarithmic scale

Taxa recorded and frequency of occurrence

The following taxa were regularly recorded from samples collected in the course of the survey; in association with each taxon, the authority (where appropriate), frequency of occurrence in samples, and the shorthand identifier used in subsequent analyses are recorded (Table 1.4).

In addition to the above, the following taxa were encountered on rare occasions;

Copepoda	<u>Eurytemora velox</u> <u>Corycaeus anglicus</u> <u>Acartia bifilosa</u> <u>Acartia discaudata</u> <u>Pseudocalanus parvus</u>	Annelida	<u>Syllid</u> sp. <u>Aphroditid</u> larvae
		Mollusca	Nudibranch juveniles
		Hydrozoa	<u>Steenstrupia</u> sp. <u>Sarsia</u> sp.
Amphipoda	<u>Gammarus zaddachi</u> <u>Hyale</u> sp. <u>Orchestia</u> sp. <u>Chaetogammarus</u> sp. <u>Corophium</u> sp.	Cladocera	<u>Evadne</u> sp.
		Teleost	<u>Pomatoschistus</u> sp.

Oligochaeta

Acaridae

Turbellaria

Nematoda

Foraminifera

Table 14 Taxa recorded, frequency of occurrence in samples, and condensed taxon identifier

Taxon	Authority	% occurrence	Identifier
Eurytemora affinis	(Poppe)		
Adult		81.1	EAFF ADUL
copepodite		89.4	EAFF COPE
Nauplii		85.0	EAFF JUVE
Harpacticid copepods		85.0	HARP SPEC
Rotifera		73.1	ROTI SPEC
(mainly Synchaeta sp.)			
Copepod nauplii (unidentified)		73.6	COPE NAUP
Neomysis integer	(Leach)	20.7	NEOM INTE
Diaptomus gracilis	Sars	24.2	DIAP GRAC
Daphnia sp.		13.2	DAPH SPEC
Bosmina sp.		18.5	BOSM SPEC
Chydorid spp.		4.0	CHYD SPEC
Cyclopoid spp.		10.6	CYCL SPEC
Acartia bifilosa inermis	Rose	20.3	ACAR INER
Acartia tonsa	Dana	15.4	ACAR TONS
Acartia longiremis	Lilljeborg	15.9	ACAR LONG
Acartia clausi	Giesbrecht	8.8	ACAR CLAU
Acartia sp. copepodites		46.2	ACAR COPE
Oithona similis	Claus	39.6	OITH SIMI
Pseudocalanus elongatus	(Boeck)	29.5	PSEU ELON
Temora longicornis	(O.F.Muller)	31.3	TEMO LONG
Centropages hamatus	Lilljeborg	11.0	CENT HAMA
Sagitta elegans	Verril	9.7	SAGI ELEG
Oikopleura sp.		6.2	OIKO PLEU
Calanus helgolandicus		4.9	CALA HELG
Littorina littorea	(L.)		
egg capsules		25.5	LITT CAPS
veligers		11.9	LITT VELI
Cirripede nauplii		51.5	CIRR NAUP
cyprids		20.3	CIRR CYPR
Terebellid larvae		10.6	TERE LARV
Polydora larvae		29.5	POLY CILI
Eteone sp. larvae		4.8	ETEO LARV
Maranzelleria wireni			
larvae		22.5	MARA WIRE
eggs		8.4	MARA EGGS
trochophores		7.0	MARA TROC
Bivalve larvae		8.4	BIVA LARV

In terms of frequency of occurrence, E.affinis, harpacticid copepods, unidentified copepod nauplii (predominantly harpacticid) and rotifers dominated the survey; all these categories were found in excess of 70% of samples. The next most frequently occurring taxa were the neritic copepods Oithona similis, Temora longicornis and Pseudocalanus elongatus, accounting for 30-40% of samples. Compound taxa such as cirripede nauplii (predominantly Balanus and Elminius but not differentiated) and the nauplii of the Acartia genus were also present in a large proportion of samples.

The Acartia species complex was well-represented in these littoral samples (6 species in all); Taylor (1987) found a similar range of species in his contemporary study of the plankton of the main channel of the Forth.

Distribution of taxa in samples

The distribution of species with respect to sample category was initially assessed by tabulating the number of samples within each category in which a species occurred (Table 1.5) and then testing (chi-squared test) whether the distribution of occurrences between related categories deviated from the overall distribution of samples between categories (Table 1.6). This approach is relatively insensitive to hierarchical structure; variation between one set of categories within another is likely to be obscured.

Table 15 The distribution of species between tide and station categories

Taxon	Category													
	High	Low	Spring	Neap	HS	LS	HN	LN	FA	SA	DU	KI	SK	CU
DAPH SPEC	13	17	13	17	4	9	9	8	16	7	5	2	0	0
BOSM SPEC	14	27	19	22	6	13	8	14	19	9	8	4	1	0
DIAP GRAC	21	33	22	32	8	14	13	19	21	20	7	6	0	0
CYCL SPEC	8	16	14	10	5	9	3	7	9	7	5	2	1	0
CHYD SPEC	1	9	7	3	1	6	0	3	6	4	0	0	0	0
NEOM INTE	14	33	22	24	8	14	5	19	8	15	16	7	1	0
EURY AFFI	134	86	111	109	71	40	63	46	41	49	47	45	20	18
ACAR CLAU	18	2	9	11	9	0	9	2	0	1	1	9	6	3
ACAR LONG	30	6	20	16	18	2	12	4	2	3	10	12	3	6
ACAR TONS	26	8	22	12	19	3	7	5	1	5	9	7	6	6
ACAR BIFI	1	0	1	0	1	0	0	0	0	0	0	1	0	0
ACAR INER	43	3	30	16	28	2	15	1	2	4	10	10	14	6
ACAR DISC	4	0	2	0	2	0	2	0	0	0	0	1	2	1
PSEU ELON	51	6	29	28	28	1	23	5	2	7	17	16	15	10
OITH SIMI	76	14	55	35	51	4	25	10	1	11	20	28	15	15
CENT HAMA	24	2	17	9	16	1	8	1	0	0	7	8	4	4
CALA HELG	11	0	7	4	7	0	4	0	0	1	2	2	3	3
TEMO LONG	63	8	42	29	40	2	23	6	0	5	15	24	15	12
PARA PARV	3	1	2	2	2	0	1	1	0	0	1	2	1	0
SAGI ELEG	22	0	17	5	17	0	5	0	0	0	4	3	12	3
OIKO DIOI	11	1	11	1	10	1	1	0	0	0	2	3	4	3
ROTI SPEC	98	68	82	84	49	33	49	35	35	44	45	31	13	7
HARP SPEC	113	79	96	96	57	39	56	40	36	44	36	40	19	20
POLY CILI	56	11	38	29	32	6	24	5	5	11	10	18	11	12
MARA WIRE	28	23	29	22	16	13	13	9	7	11	13	12	4	4
MARA TROC	12	4	12	4	9	3	3	1	0	2	3	8	1	2
MARA EGGS	12	7	15	4	9	6	3	1	2	4	4	6	1	2
LITT CAPS	41	17	33	25	26	7	15	10	8	7	12	10	8	13
LITT VELI	24	4	17	11	15	2	9	2	1	4	5	6	5	6
APHR LARV	2	4	6	0	2	4	0	0	0	0	1	5	0	0
SYLL SPEC	3	0	2	1	2	0	1	0	0	0	0	1	2	0
ETEO LARV	5	6	8	3	4	4	1	2	0	2	3	5	1	0
TERE LARV	19	5	13	11	11	2	8	3	0	4	3	9	3	5
NERE LARV	15	9	18	6	11	7	4	2	3	4	7	5	3	2
CIRR CYPR	36	10	30	16	26	4	10	6	2	8	9	13	6	8
CIRR NAUP	93	24	64	53	55	9	38	15	3	14	26	39	16	19
BIVA LARV	11	8	9	10	5	4	6	4	0	0	2	12	4	1

Table 1.6 Association of taxa with tidal and geographical sample categories. +,- indicate a significant chi-squared value; the sign indicates whether a taxon could most easily be considered biased towards or away from a particular category

Taxon	Tides								Station					
	H	L	S	N	HS	LS	HN	LN	FA	SA	DU	K	SK	CU
DAPH SPEC		+							+					
BOSM SPEC		+				+			+					
DIAP GRAC		+				+			+					
CYCL SPEC		+				+							-	-
CHYD SPEC		+				+			+					
NEOM INTE		+						+		+	+			
EURY AFFI														
ACAR CLAU	+									+				
ACAR LONG	+				+		+				+	+		
ACAR TONS	+				+				-					
ACAR BIFI														
ACAR INER	+		+		+		+		-	-				
ACAR DISC														
PSEU ELON	+				+		+		-	-				
OITH SIMI	+				+				-	-				
CENT HAMA	+		+		+		+		-	-				
CALA HELG	+				+		+		-	-			+	+
TENO LONG	+				+		+		-	-				
FARA PARV														
SAGI ELEG	+		+		+		+						+	
OIKO DIOI	+		+		+				-	-			+	+
ROTI SPEC														
HARP SPEC														
POLY CILI	+				+		+		-				+	
MARA WIRE									-					
MARA TROC													+	
MARA EGGS														
LITT CAPS					+									+
LITT VELI	+				+		+						+	+
AFHR LARV			+										+	
SYLL SPEC													+	+
ETEO LARV					+						+	+		
TERE LARV														+
NERE LARV			+						-	-				
CIRR CYPR	+				+				-					
CIRR NAUP	+				+				-					
BIVA LARV									-				+	

High/low tides

Comparison of high and low tide occurrences revealed two readily-distinguished groups; those which occurred significantly more frequently than expected on high tides and those which showed a similar bias towards low tides.

The former group comprised mainly neritic calanoid copepods - Acartia spp., Pseudocalanus, Oithona, Centropages, Calanus and Temora- together with Oikopleura, Sagitta and some lower-estuary meroplanktonic forms (Littorina egg capsules, cirripede larvae and Polydora larvae). The second group comprised predominantly freshwater holoplankton including Daphnia, Bosmina, cyclopoid copepods, chydorids and the upper-estuarine mysid Neomysis.

Spring/neap tides

The majority of taxa had occurrences more or less evenly divided between spring and neap tide samples (Table 1.5). Only four groups showed a deviation from the relative frequency of occurrence of spring and neap samples. The marine genera Sagitta and Oikopleura both occurred significantly more frequently than expected on spring tides, as did the larvae of aphroditid and nereid polychaetes.

High and low spring/high and low neap tides

This comparison refines the evidence from the two previous comparisons. The neritic copepods occurred significantly more frequently than expected on

high spring tides, as did Sagitta and Oikopleura. Aphroditid larvae were significantly associated with low spring tides, as were the freshwater holoplankton.

Littorina egg capsules and veligers, and cirripede nauplii and cyprid larvae were both significantly associated with high spring tides.

Comparison between stations

Twenty-eight out of forty-two taxa showed a significant degree of association with station (Table 1.5, Table 1.6). Neritic copepods were most strongly associated with Dunmore and Kincardine (Fig.1.2), whilst freshwater cladocera and copepods were strongly associated with Fallin and S.Alloa. Neomysis appeared significantly more often in S.Alloa and Dunmore samples than in collections from other stations. Meroplanktonic larvae occurred significantly less frequently at the up-estuary stations Fallin and S.Alloa than the relative number of samples taken at each station would predict. Maranzellaria larvae were most strongly associated with Dunmore and Kincardine, while littorinid and cirripede larvae were biased towards the lower-estuary sites Culross and Skinflats. Sagitta and Oikopleura were also biased towards the lower-estuary stations.

Spatial and temporal patterns of abundance of individual species

Raw abundance data (individuals/cubic metre) were tabulated by station and tide (Appendix B), and abundances of selected taxa plotted on logarithmic or linear scales as appropriate to the abundance levels recorded (Appendix C, Figs.C1 to C19).

The contents of Appendices B and C are intended primarily for reference, and will not be interpreted in detail. Six taxa have been omitted from tabulation in Appendix B; Syllid larvae, Paracalanus sp., Acartia bifilosa, Acartia discaudata, nudibranch juveniles and aphroditid larvae all occurred in less than four percent of samples.

Seasonal plots of abundance were constructed station-by station for the following five categories (holoplanktonic taxa chosen on the basis of abundance and/or their relative importance within a particular planktonic association):

E.affinis : Nauplii
Copepodites
Adults

Freshwater : Diaptomus
Daphnia
Bosmina
Chydoridae

Mixed taxa : Unassigned copepod nauplii

Neomysis

Harpacticid copepods

Rotifera

Acartia genus : A. clausi

A. longiremis

A. tonsa

A. bifilosa inermis

Neritic copepods : Temora longicornis

Centropages hamatus

Oithona similis

Pseudocalanus elongatus

Meroplankton

Several meroplanktonic taxa showed strongly seasonal patterns of abundance. This was especially marked for the eggs and larvae of Littorina, cirripedes, and the spionids Maranzelleria and Polydora. Littorinid egg capsules were largely confined to Culross between March and July 1982 (upto 4343/m-3) although 692 m-3 were present on 15.12.82 at Culross (Table B6). Cirripede nauplii displayed a similar pattern of abundance but a longer period of occurrence at Culross (Table B6), and were also abundant over the same

period (March-September) at Kincardine and Skinflats. At each station at which they occurred regularly, both Littorina capsules and cirripede nauplii displayed a pattern of relatively higher abundance on high spring tides than on high neap tides.

Larvae of Maranzelleria were confined to a period in March-April 1982, and were most abundant (up to 160000 m⁻³) at Skinflats although occurring at all stations including Fallin. Larvae of terebellid polychaetes, Polydora, Eteone and bivalves attained both maximum frequency of occurrence and maximum abundance in May 1982 (Tables B 4 to 6). The spionids Maranzelleria and Polydora displayed a succession of larval production.

E.affinis

The pattern of abundance of E.affinis will be described below in conjunction with consideration of the population size and age structure.

Freshwater taxa

The influence of the freshwater community extended, with diminishing magnitude, as far down-estuary as Kincardine (Figs.C16 to C19). Abundances were generally low for all taxa, rarely exceeding 200m⁻³. There was a trend, becoming more marked down-estuary, for abundances to be greater on low tides than on high tides. At Fallin, S.Alloa (except Diaptomus on low tides) and Dunmore. Diaptomus, Daphnia and Bosmina were most abundant

during the period January-April, whilst chydorids were most abundant during the period September-November. Chydorids appeared at Dunmore in only one sample (low tide), and were absent from all Kincardine, Culross and Skinflats samples. The pattern of abundance of Diaptomus, Daphnia and Bosmina at Kincardine on low tides was similar to that further up-estuary.

Acartia genus

Members of the Acartia genus occurred on only five occasions at Fallin (Table B1). The abundances of A.clausii, A.longiremis, A.bifilosa inermis and A.tonsa have been plotted for high and low tides for S.Alloa, Dunmore and Kincardine, and for high tides at Culross and Skinflats (Figs. C11-15).

A.clausii occurred infrequently, in low numbers and predominantly on high tides at all the above stations, exceeding 300 m⁻³ only once (Skinflats, March 1982). A similar spring maximum occurred at Kincardine; at the remaining stations, maximum abundance occurred towards the end of the year (Fig. C13).

A.longiremis exceeded 100 m⁻³ only once, at Kincardine in July 1982. The remaining occurrences were patchily distributed in time and most frequent at Culross and Kincardine. Occurrences were predominantly on high tides. At Culross and Skinflats, A.longiremis was most common in the latter half of the year (Figs. C14,15), but at Dunmore and S.Alloa occurred most frequently between May and July 1982. Occurrence was distributed over a longer period of time at Kincardine than at other stations, with a number of appearances in low tide samples.

A.bifilosa inermis occurred at all stations in generally low abundances and in no obvious pattern. Numbers of over 1100 m⁻³ were recorded in a single May sample at Skinflats, and reached 225 m⁻³ at Kincardine on the same occasion (Table B4,5;Fig.C13,14); abundance did not otherwise exceed 100m⁻³ at any station. Low tide occurrences were rare.

A.tonsa appeared at all stations except Fallin from September onwards. This species showed considerable overlap in occurrence with A. longiremis.

Neritic copepods

Temora, Centropages, Oithona and Pseudocalanus (Table B1-6;Figs C6-10) showed no clear seasonal pattern of abundance, and there was little correspondence in occurrences between stations. At Dunmore and S.Alloa, Centropages had peak abundance in May. At Culross and Skinflats, Centropages showed a similar peak, but at both stations the maximum Pseudocalanus numbers occurred in November. At Kincardine, Centropages and Pseudocalanus were abundant only in November and December 1982.

Temora and Oithona showed intermittent peaks of abundance throughout the year.

Mixed Group

Of the four taxa in this group, only Neomysis and the rotifers will be considered here. Harpacticid copepods are predominantly benthic in habit,

and were present in samples mainly as a consequence of resuspension. Although, by definition in this study, the mixed copepod nauplii were not fully identified, the majority were of harpacticid species.

Neomysis occurrence was most frequent, and abundance highest, at S.Alloa. The mysid occurred only in low tide samples at Kincardine, was rare at Skinflats and absent from Culross samples. Only at S.Alloa did Neomysis occur during the early part of the year (Table B3; Fig C2a,b). At Fallin and all other sites, Neomysis appeared only from May-July onwards, with maximum abundances occurring at most sites in September.

Rotifera (predominantly Synchaeta sp. , but including freshwater species such as Keratella and Polyarthra) occurred in high numbers at all stations (except Culross) between December 1981 and February 1982. Highest abundances were recorded at S.Alloa during this period, when numbers exceeded 300000 m⁻³ (Table B3). Rotifera occurred almost exclusively in the 69 um net fraction.

Patchiness: spatial and temporal variation in abundance
and distribution on the scale of sampling

Spatial variation

The position of the buoys used to mark the limits of the sampling grid was checked, using a hand-bearing compass, during low tide on the day following sampling. Within the limits of resolution of the method, the grid was found to be approximately 120m square and oriented N-S E-W.

E.affinis, Polydora larvae, and Acartia clausi were found to be sufficiently numerous in the approximately 80 l samples for their distribution to be modelled; these groups, together with total number of taxa, salinity and temperature, were contoured using computer routines supplied by the GINOSURF package.

The resulting plots are rather idealised, since each sample is treated as a single point rather than as a segment of a transect. They nonetheless serve to give some indication of the presence and dimensions of plankton patches in the littoral zone. In interpreting these contour plots, it should be borne in mind that the adjacent shoreline runs N-S, and that therefore the horizontal axis of the plots is parallel to the shore.

Both salinity and temperature display a distinct front parallel to the shore (Fig.1.13e,f) Beyond 80 m from the inshore edge of the grid, both variables were relatively constant at >26‰ and 11.5 deg.C respectively. Moving inshore, salinity decreased rapidly to 19‰ over a distance of 20m, and temperature increased to 14.0 deg.C. Within 40m of the westerly edge of

the grid, salinity had fallen to 16‰, but with some suggestion that the low-salinity water was bounded to the south by a wedge of higher-salinity water. Since sampling was conducted in about 1.5 m of water, and sample bottles were immersed to a depth of 50 cm, it is unlikely that this pattern could be attributed simply to a shallow layer of low-salinity water overlying more saline water.

The number of taxa present (Fig.1.13d) was reduced within the front, increasing both inshore and, to a greater extent, offshore.

The three taxa represented have been contoured in numbers/100l, and showed differing patterns of distribution. Polydora larvae showed a relatively small range of abundance (20-60/100l); the contours indicated patch sizes of between 30 and 100m radius (Fig.1.13c), with parts of up to four patches present within the grid. One patch appeared to be located within the front itself.

In contrast, E.affinis ranged in abundance from less than 5 to more than 55 per 100 l, and the main patch (Fig.1.13a) did not appear to cross the front. This patch had dimensions of 60-100m, and was oblate in a N-S direction. Although E.affinis is generally associated with lower-salinity water, in this instance the main concentration of numbers was on the high salinity side of the front.

A.clausii displayed yet another pattern distribution. Numbers were at a minimum of about 50/100l within the front. To either side of the front, patches of 40-100m diameter, with up to five times this minimum had developed. Substantial numbers were therefore associated with both cooler, high-salinity water and with warmer, low-salinity water.

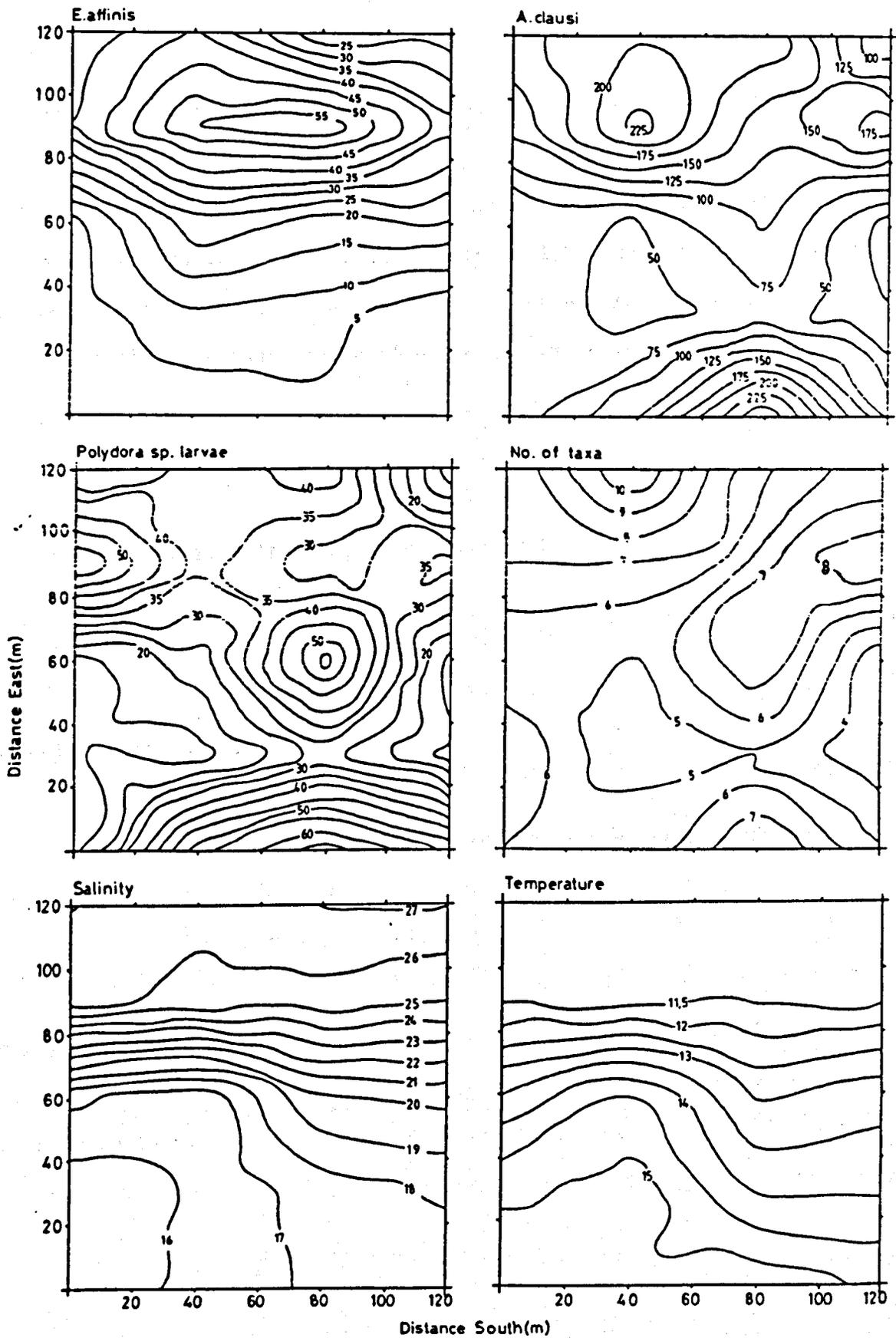


Figure 1.13 Small-scale spatial variation in zooplankton distribution, salinity, and temperature within a 120m square grid at Skinflats. Zooplankton abundance contoured in nos./100l.

Temporal variation

In a series of 8 consecutive 500l samples taken at Dunmore on 3.3.83, numbers of E.affinis ranged from 137 m-3 to 909 m-3, with an arithmetic mean of 496 m-3. The maximum abundance occurred in the middle of the sample series, with numbers rising and falling more or less monotonically on either side. The 95% confidence interval for a single sample (expressed as a percentage of the mean was calculated using the approximation:

$$\text{C.I.} = \frac{[\text{antilog } (y \pm 2s)] \times 100}{\text{antilog } y}$$

antilog y

(Gagnon and Lacroix, 1982)

where s = standard deviation of the log-transformed values

y = geometric mean

This gave limits of 29-347% of the mean, and indicated that abundances in samples taken over longer time intervals would need to differ by a factor of 3.5 or more to be considered significantly different.

Eurytemora affinis: field observations

Effects of preservation on length

A comparison between the length distributions of subsamples of preserved and unpreserved female E.affinis indicated that Steedman's solution had no measurable effect on cephalothorax length. Consequently, no correction was made to the lengths recorded from preserved specimens from the field survey.

Variation in length between tides and stations

In order to simplify the process of obtaining stage-specific length data for E.affinis throughout the year, it was necessary to establish whether samples from a single station and tidal state could be considered representative of the upper estuary as a whole. To this end, the size distribution of male and female adults was plotted for Fallin, S.Alloa and Dunmore, on high and low tides, on consecutive spring and neap tides (17.5.82, 24.5.82, 31.5.82).

On 17.5.82 there was no verall difference in size distribution between stations or tides (Fig.1.14), although the modal length of males in the low tide Dunmore sample was greater than at the up-estuary stations. The modal length of males was consistently less than females.

On 24.5.82 and 31.5.82 , there was again no obvious pattern of difference

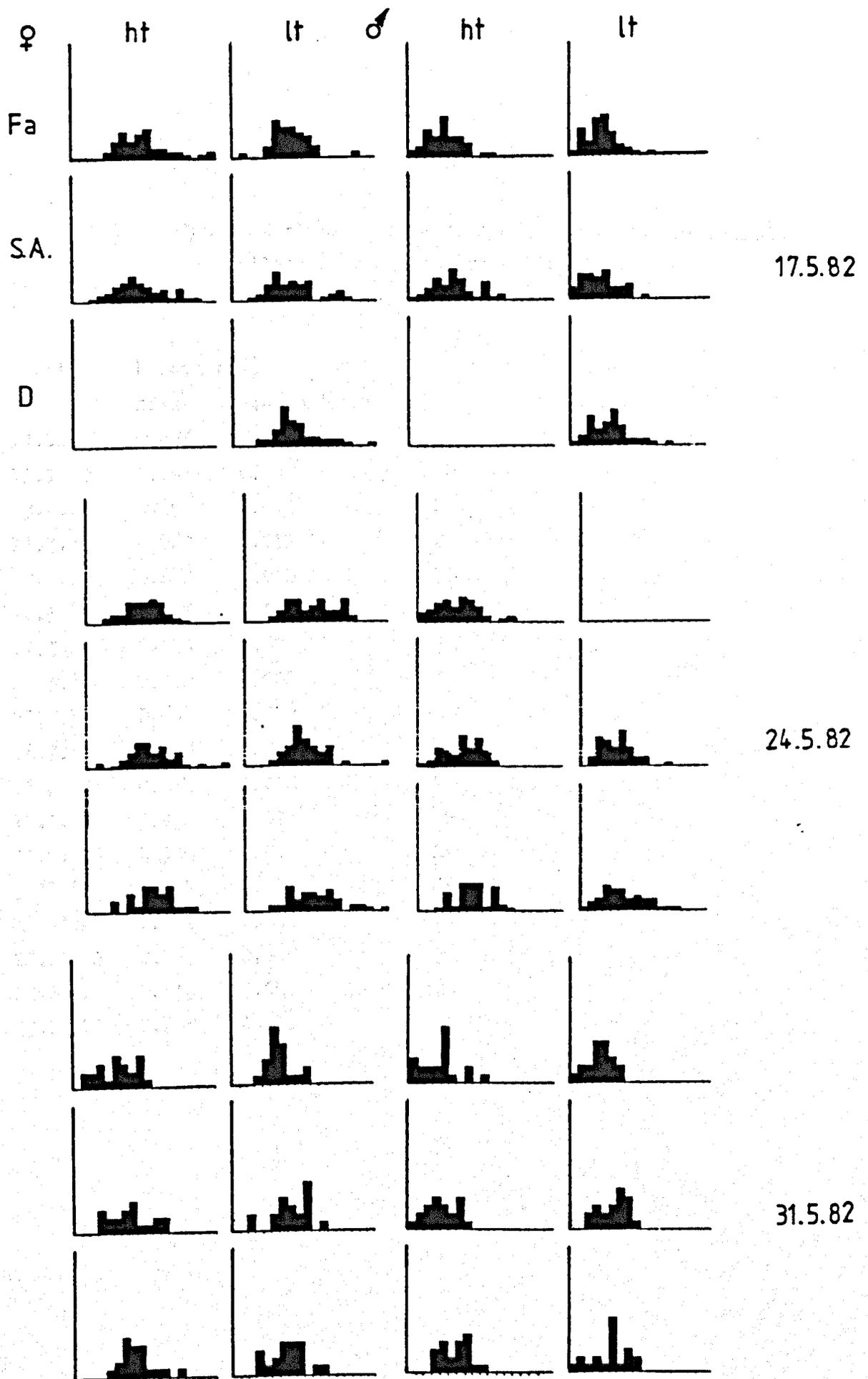


Figure 1.14 Size-frequency histograms of male and female adult *E.affinis* collected on high and low tides at Fallin, S.Alloa and Dunmore on 17, 24 and 31 May 1982

Table 1.7 Mean cephalothorax length of C6 female E. affinis collected at HT S.Alloa on 18 dates

Date	Length (mm)		n
	mean	standard error	
11.12.81	0.836	0.010	17
12.1.82	0.841	0.007	30
13.2.82	0.898	0.015	20
11.3.82	0.882	0.011	20
2.4.82	0.842	0.010	30
10.5.82	0.736	0.010	30
17.5.82	0.719	0.008	50
24.5.82	0.712	0.008	50
31.5.82	0.694	0.010	20
8.7.82	0.693	0.007	30
6.9.82	0.951	0.010	20
13.9.82	0.952	0.011	9
20.9.82	0.905	0.009	20
3.11.82	0.807	0.009	20
16.11.82	0.793	0.014	10
22.11.82	0.769	0.008	30
15.12.82	0.853	0.006	30
23.12.82	0.848	0.018	30

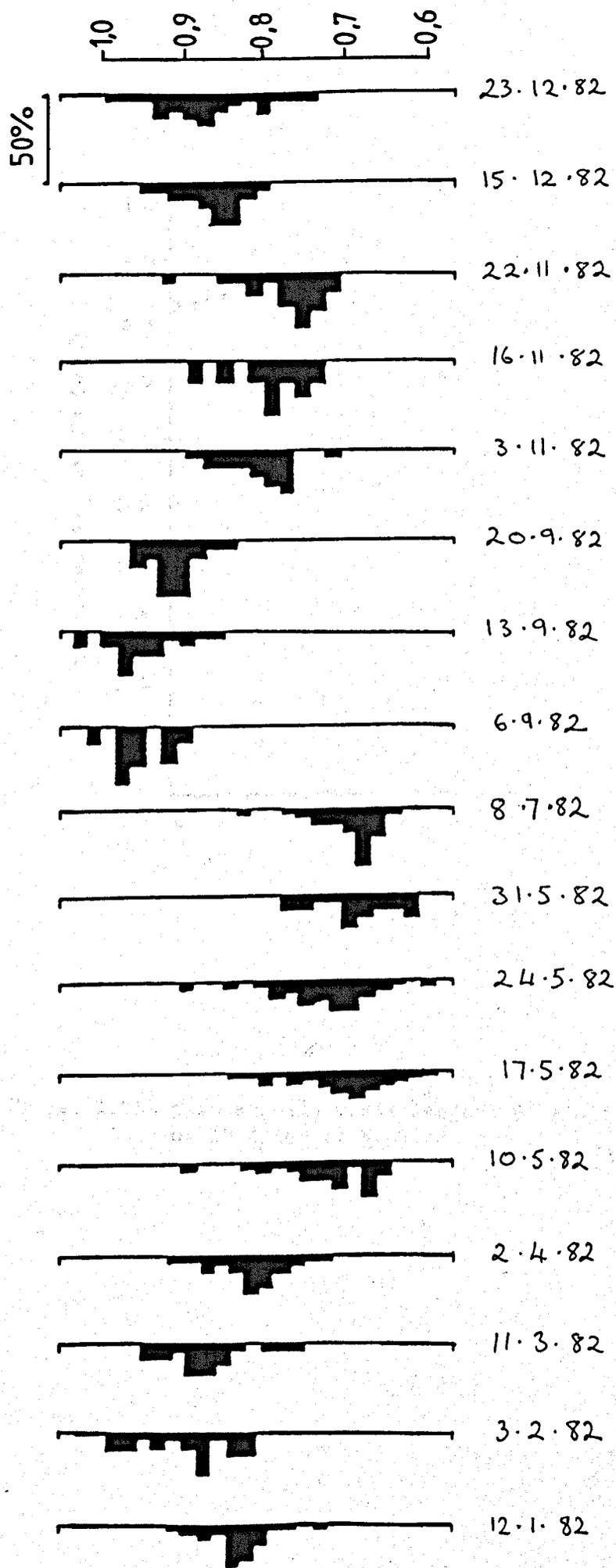
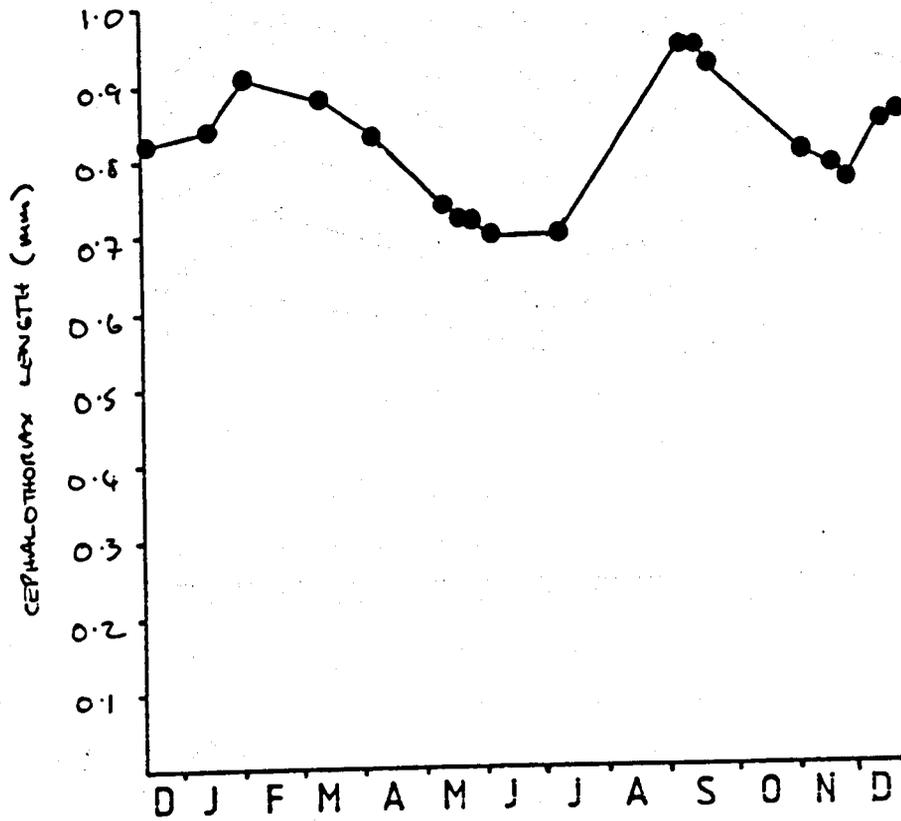


Figure 1.15a Size-frequency histograms of adult female *E. affinis* (0.018mm size classes) collected on 18 dates (see Table 1.7) at S. Alloa



C6♀ lengths 1981-2

Figure 1.15b Mean cephalothorax lengths of adult female E.affinis collected on 18 dates at S.Alloa

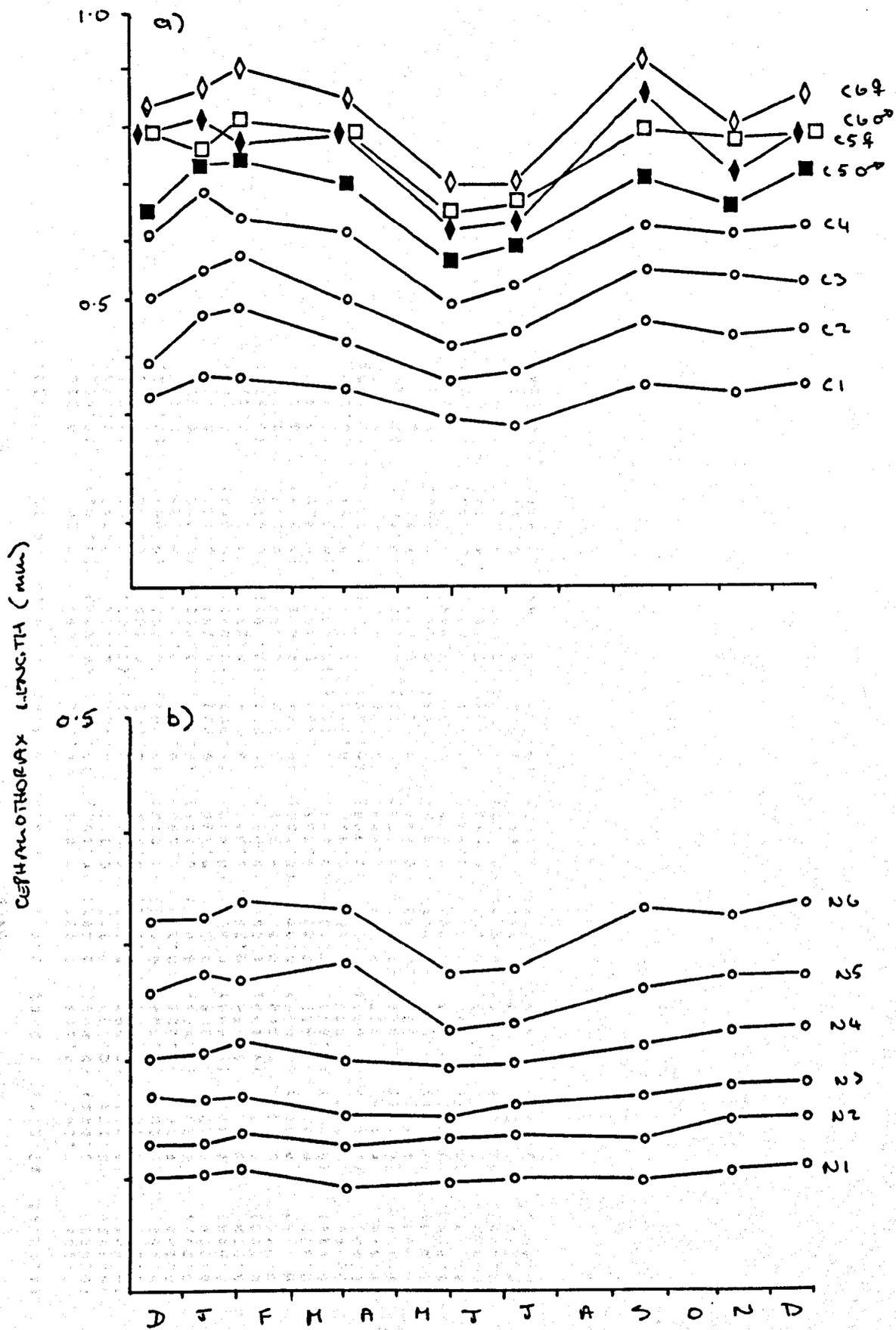


Figure 1.16 Mean cephalothorax lengths of all developmental stages of *E.affinis* collected on 9 dates at S.Alloa

Table 1.9 Mean cephalothorax (mm, S.E. in brackets) of naupliar and copepodite instars of E. affinis : high tide samples at S.Alloa on 9 dates

Stage	Date									
	11.12.81	22.1.82	3.2.82	2.4.82	31.5.82	8.7.82	20.9.82	16.11.82	23.12.82	23.12.82
n1	0.101 (0.003)	0.103 (0.001)	0.106 (0.001)	0.092 (0.001)	0.096 (0.002)	0.101 (0.002)	0.097 (0.002)	0.107 (0.002)	0.110 (0.002)	0.110 (0.002)
n2	0.126 (0.001)	0.128 (0.001)	0.135 (0.002)	0.123 (0.002)	0.133 (0.002)	0.131 (0.002)	0.131 (0.002)	0.147 (0.001)	0.144 (0.001)	0.144 (0.001)
n3	0.170 (0.002)	0.166 (0.002)	0.169 (0.004)	0.153 (0.002)	0.152 (0.002)	0.161 (0.002)	0.168 (0.003)	0.180 (0.002)	0.180 (0.002)	0.180 (0.002)
n4	0.204 (0.002)	0.207 (0.002)	0.214 (0.003)	0.199 (0.003)	0.193 (0.003)	0.194 (0.003)	0.210 (0.002)	0.223 (0.271)	0.227 (0.272)	0.227 (0.272)
n5	0.259 (0.003)	0.274 (0.003)	0.268 (0.004)	0.284 (0.004)	0.226 (0.002)	0.232 (0.003)	0.259 (0.003)	0.271 (0.002)	0.272 (0.002)	0.272 (0.002)
n6	0.318 (0.003)	0.324 (0.003)	0.338 (0.003)	0.331 (0.004)	0.273 (0.002)	0.276 (0.004)	0.330 (0.003)	0.321 (0.004)	0.335 (0.004)	0.335 (0.004)
c1	0.333 (0.005)	0.371 (0.006)	0.364 (0.005)	0.349 (0.007)	0.298 (0.006)	0.279 (0.004)	0.356 (0.006)	0.337 (0.003)	0.351 (0.005)	0.351 (0.005)
c2	0.385 (0.011)	0.460 (0.007)	0.482 (0.003)	0.423 (0.004)	0.358 (0.004)	0.369 (0.007)	0.457 (0.005)	0.428 (0.016)	0.432 (0.006)	0.432 (0.006)
c3	0.496 (0.008)	0.547 (0.007)	0.572 (0.007)	0.500 (0.009)	0.416 (0.005)	0.441 (0.004)	0.551 (0.009)	0.554 (0.008)	0.527 (0.008)	0.527 (0.008)
c4	0.610 (0.014)	0.685 (0.011)	0.637 (0.014)	0.617 (0.011)	0.489 (0.006)	0.520 (0.011)	0.628 (0.008)	0.612 (0.009)	0.621 (0.010)	0.621 (0.010)
c5f	0.786 (0.013)	0.817 (0.012)	0.772 (0.012)	0.793 (0.011)	0.621 (0.006)	0.632 (0.009)	0.857 (0.007)	0.716 (0.006)	0.788 (0.010)	0.788 (0.010)
c5m	0.699 (0.007)	0.727 (0.007)	0.743 (0.009)	0.700 (0.008)	0.561 (0.016)	0.590 (0.006)	0.709 (0.009)	0.657 (0.009)	0.724 (0.008)	0.724 (0.008)
c6f	0.831 (0.010)	0.869 (0.008)	0.898 (0.015)	0.842 (0.010)	0.694 (0.010)	0.693 (0.007)	0.905 (0.009)	0.793 (0.014)	0.848 (0.018)	0.848 (0.018)
c6m	0.790 (0.007)	0.750 (0.010)	0.805 (0.014)	0.792 (0.018)	0.642 (0.008)	0.652 (0.008)	0.781 (0.016)	0.763 (0.014)	0.787 (0.014)	90.014

in female length between tides and stations, but again some indication that the modal length of males was greater at Dunmore.

On the basis of the above observations, S.Alloa high tide samples were selected as the source of specimens for biometric and age-structure evaluation. Mean female c6 cephalothorax length was determined for 18 dates (Table 1.7; Fig. 1.15a,b), and mean length of all stages determined for 9 dates (Table 1.9; Fig. 1.16a,b).

Female length distribution (Fig. 1.15a) was too irregular to permit the discernment of multiple generations. Both length frequency and mean length (Fig. 1.15b) displayed a bimodal temporal distribution, with peaks of 0.898mm on 3.2.82 and 0.952mm on 13.9.82. Mean length fell to 0.769mm on 22.11.82 before returning in December to levels comparable with the same period in 1981. Minimum mean length was observed in May and July samples; these were, at 0.693mm and 0.694mm respectively, some 27% less than the maximum.

The annual variation in lengths of other stages followed a similar pattern, which was most apparent in c5 and c6 and increasingly damped in earlier stages as variations fell within the limit of precision of measurement (Table 1.7; Fig. 1.16a,b). A summer minimum was still evident for n6, however. C6 females were consistently larger than other stages. For both c5 and c6, females were always larger than males. There was a degree of overlap between the lengths of c6 males and c5 females.

Abundance: upper estuary

The highest recorded abundances of E. affinis were at Fallin (exceeding 250000 m⁻³ on 24.5.82 and 31.5.82) and Dunmore (179796 m⁻³ on 2.4.82) (Table 1.8). Maximum abundance at S.Alloa was 96280 m⁻³ on 24.5.82 and at

HIGH TIDE

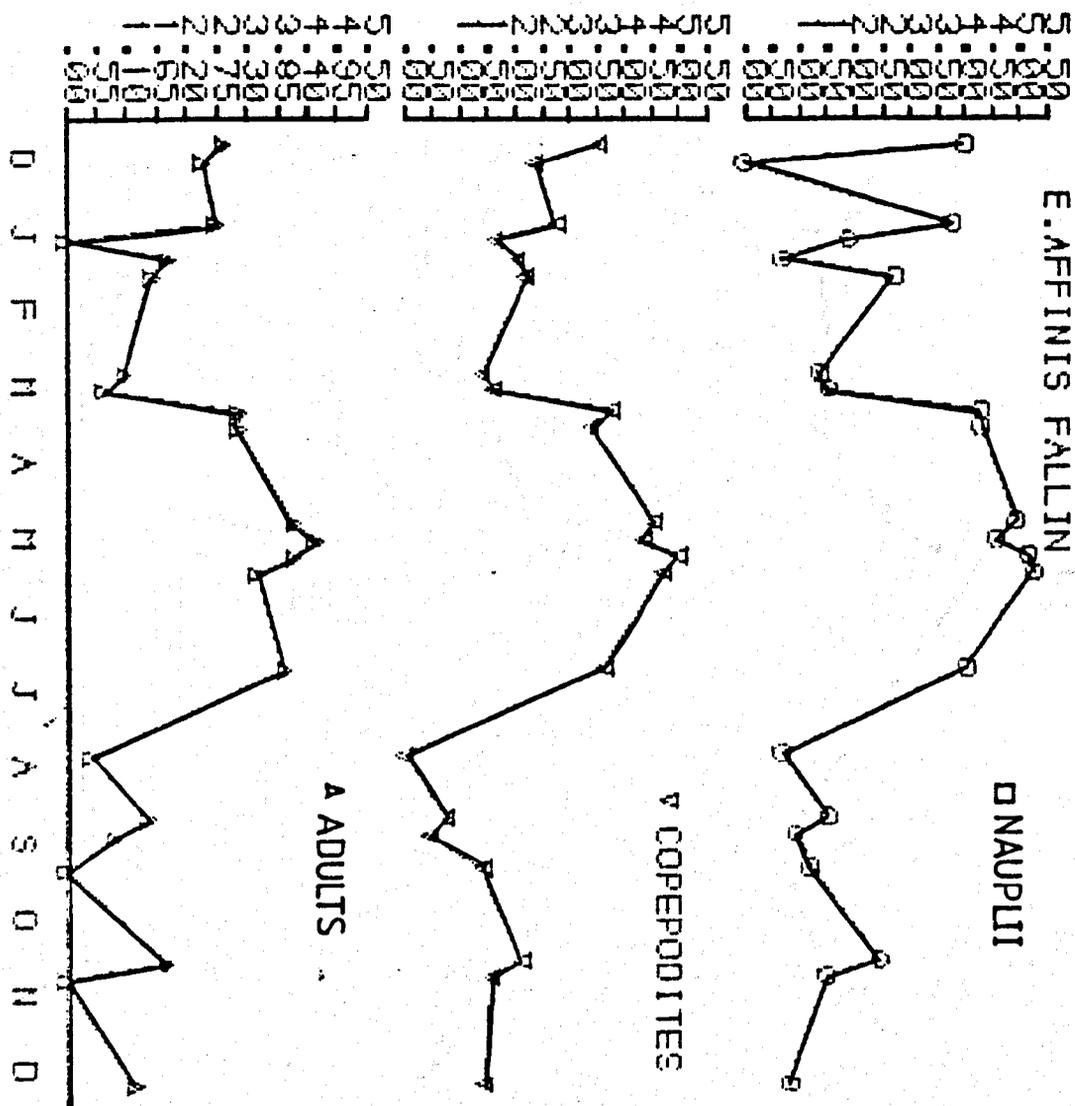


Fig. 1.17 a Abundance of E. affinis : Fallin high tide

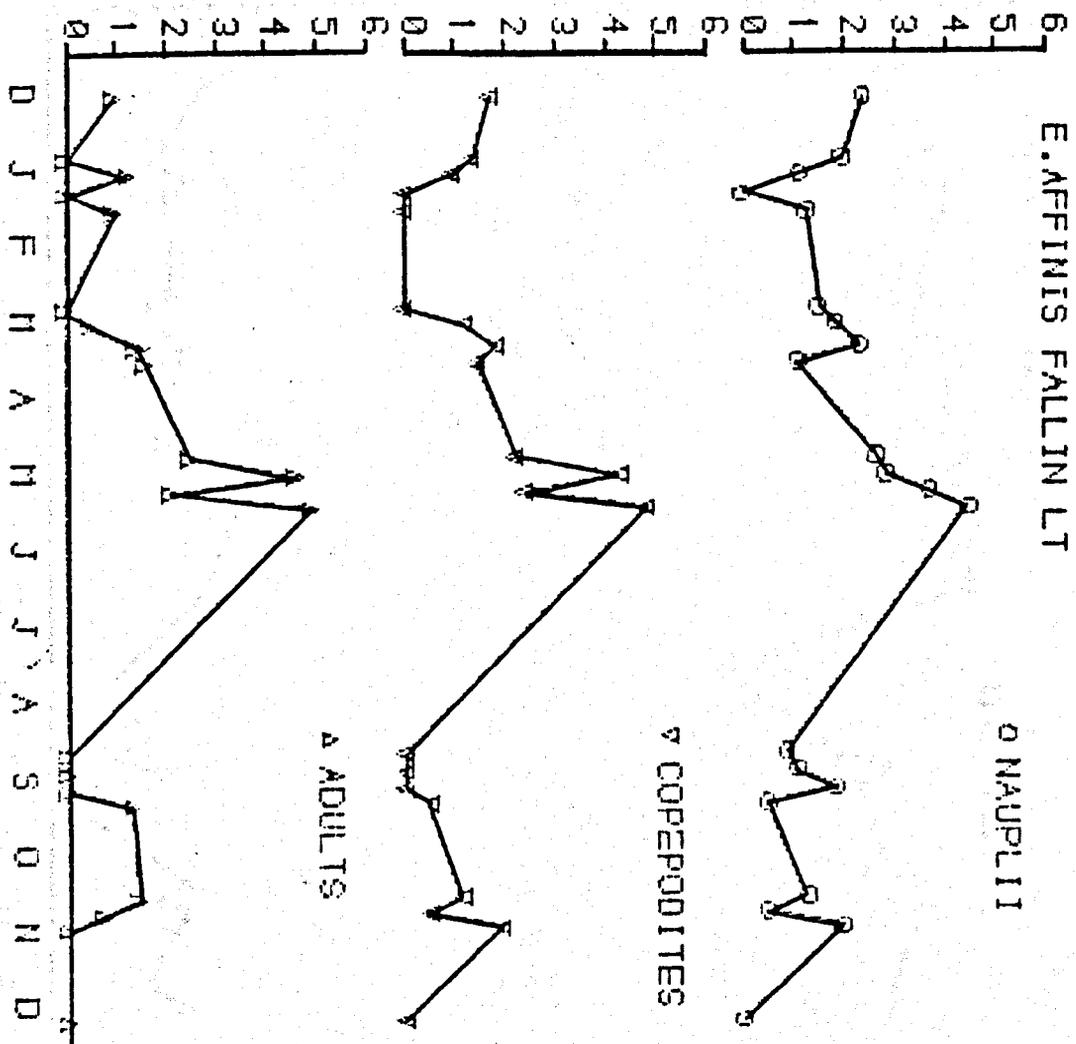


Fig. 1.17 b Abundance of E. affinis : Fallin low tide

HIGH TIDE

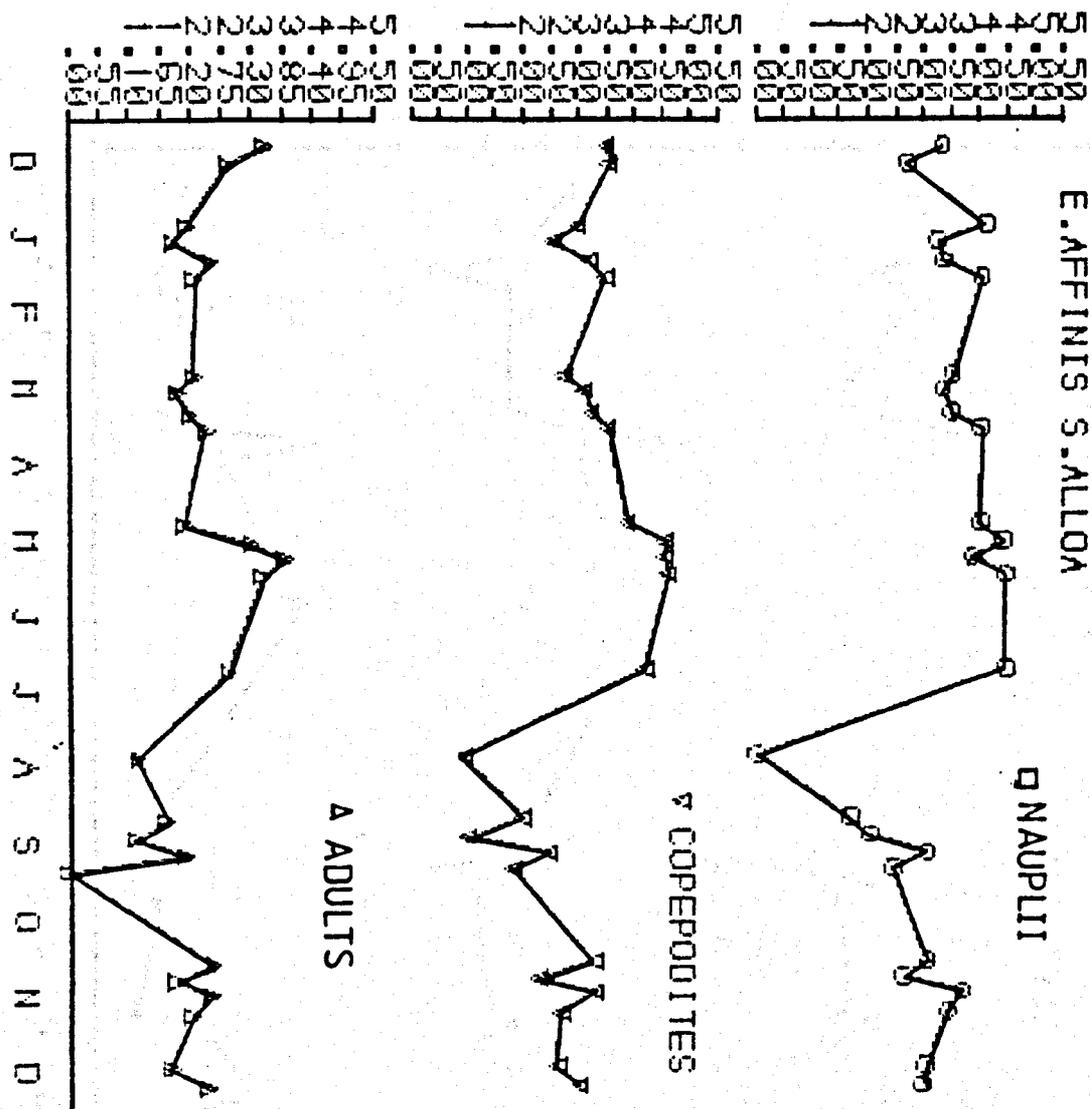


Fig. 1.18 a Abundance of E. affinis; South Alloa high tide

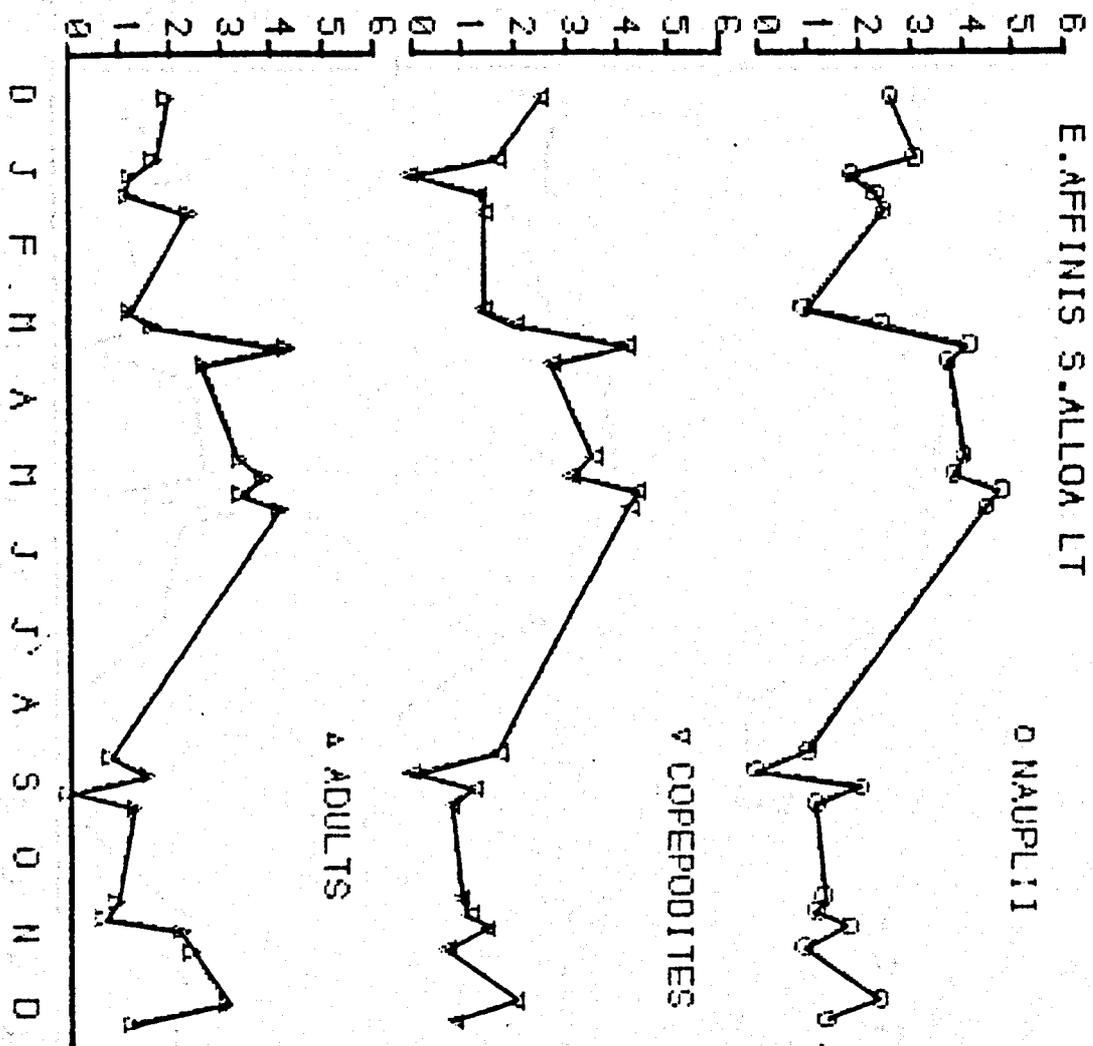


Fig. 1.18 b Abundance of E. affinis; South Alloa low tide

HIGH TIDE

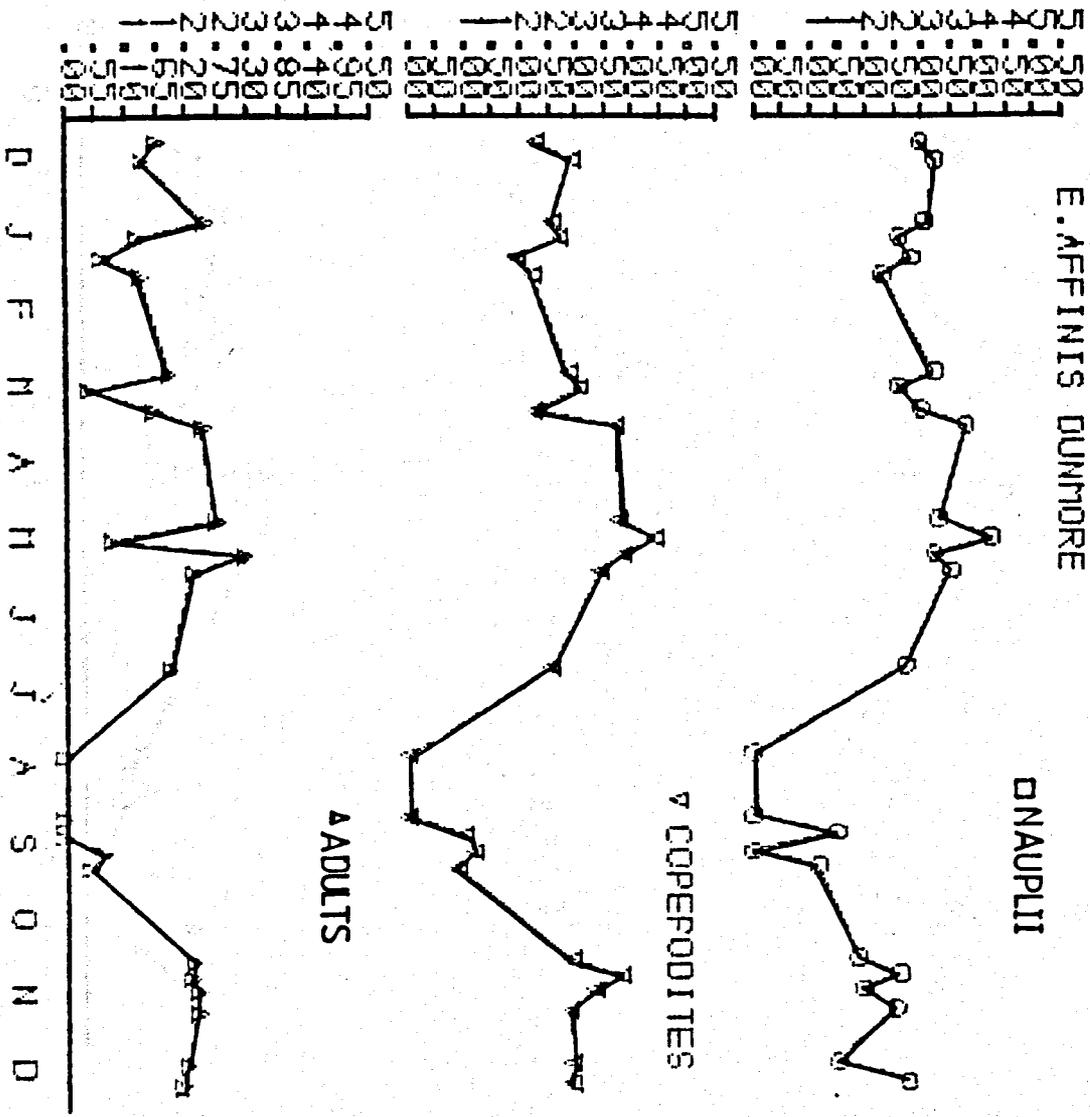


Fig. 1.19 a Abundance of E. affinis; Dunmore high tide

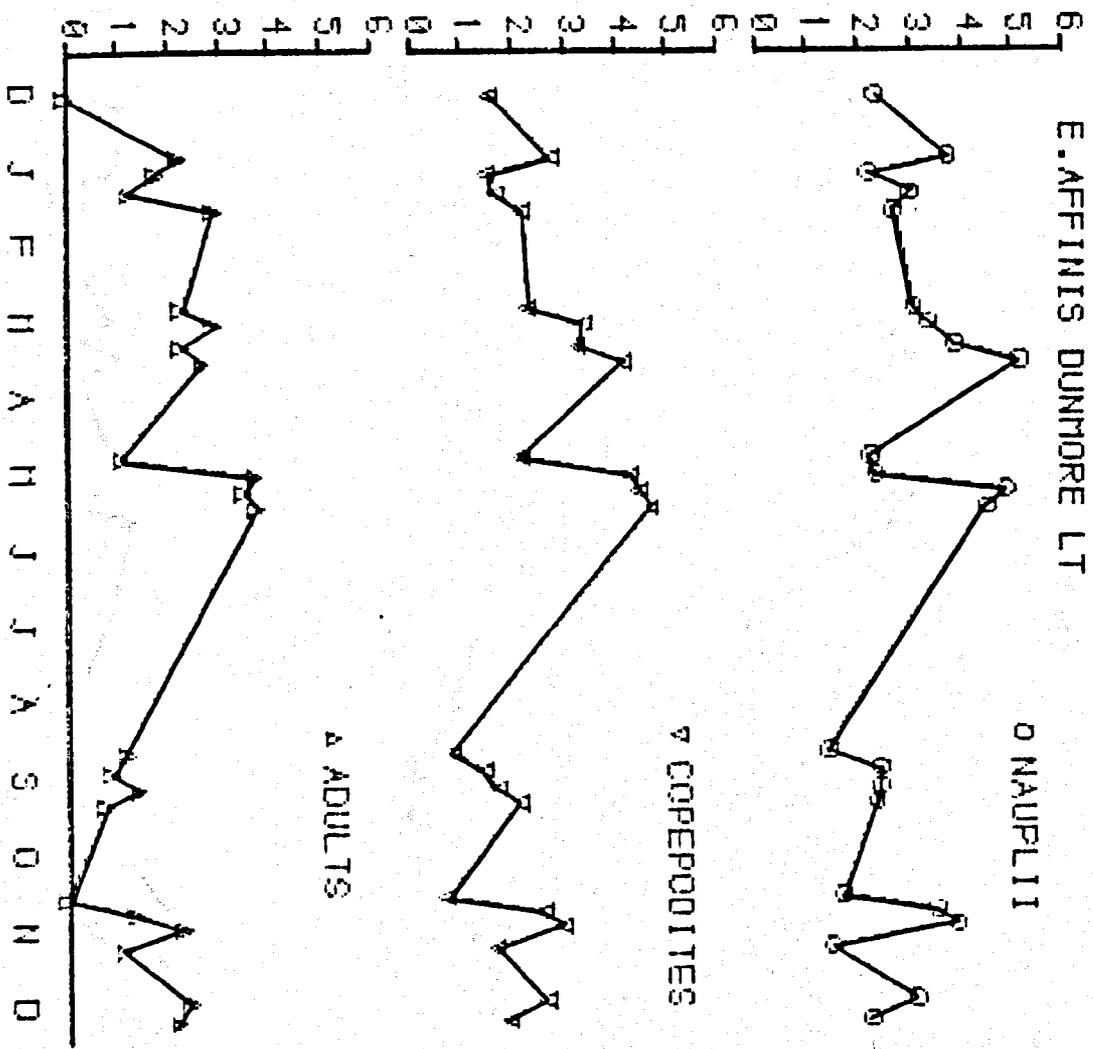


Fig. 1.19b Abundance of E. affinis:Dunmore low tide

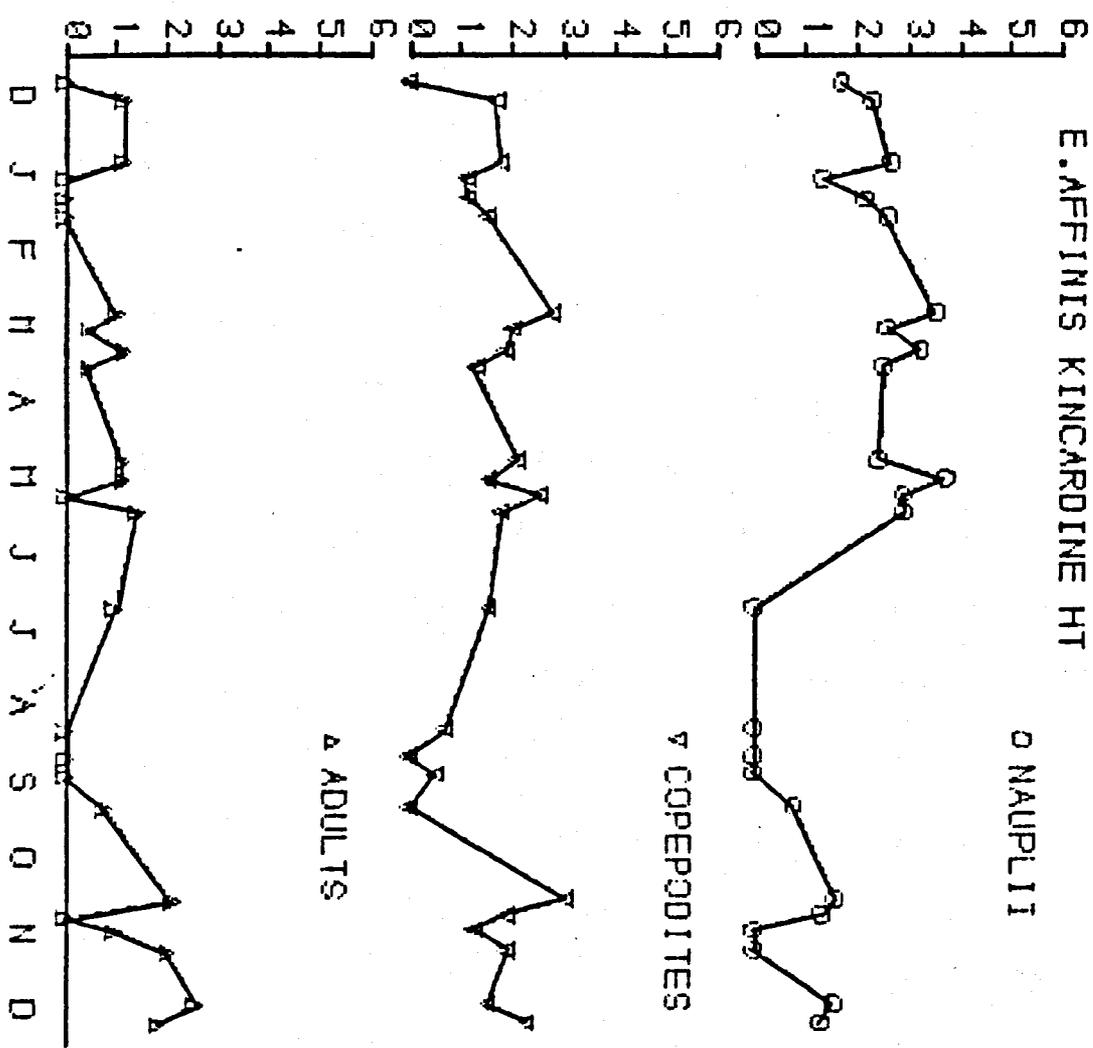


Fig. 1.20 a Abundance of E. affinis:Kincardine high tide

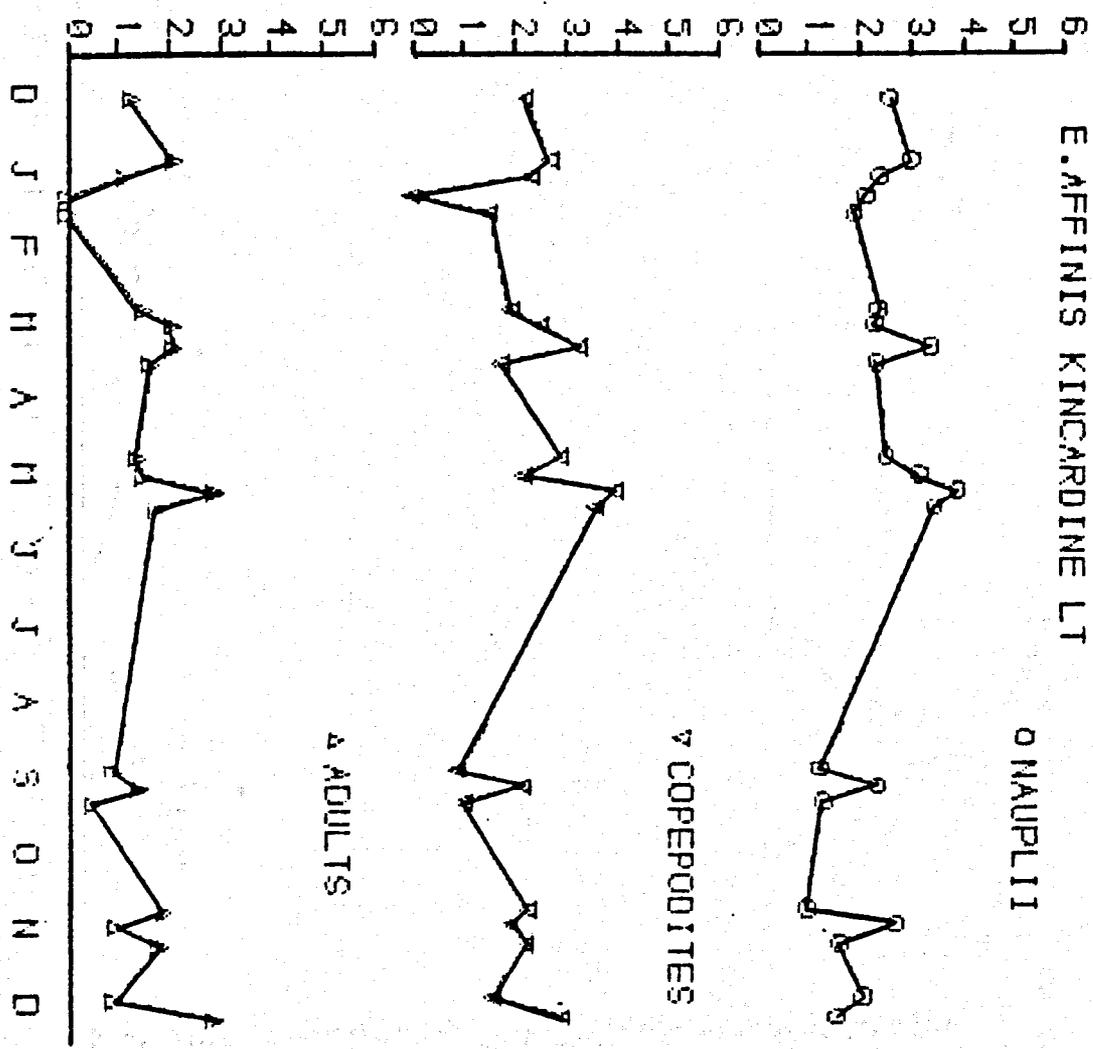


Fig. 1.20 b Abundance of E. affinis:Kincardine low tide

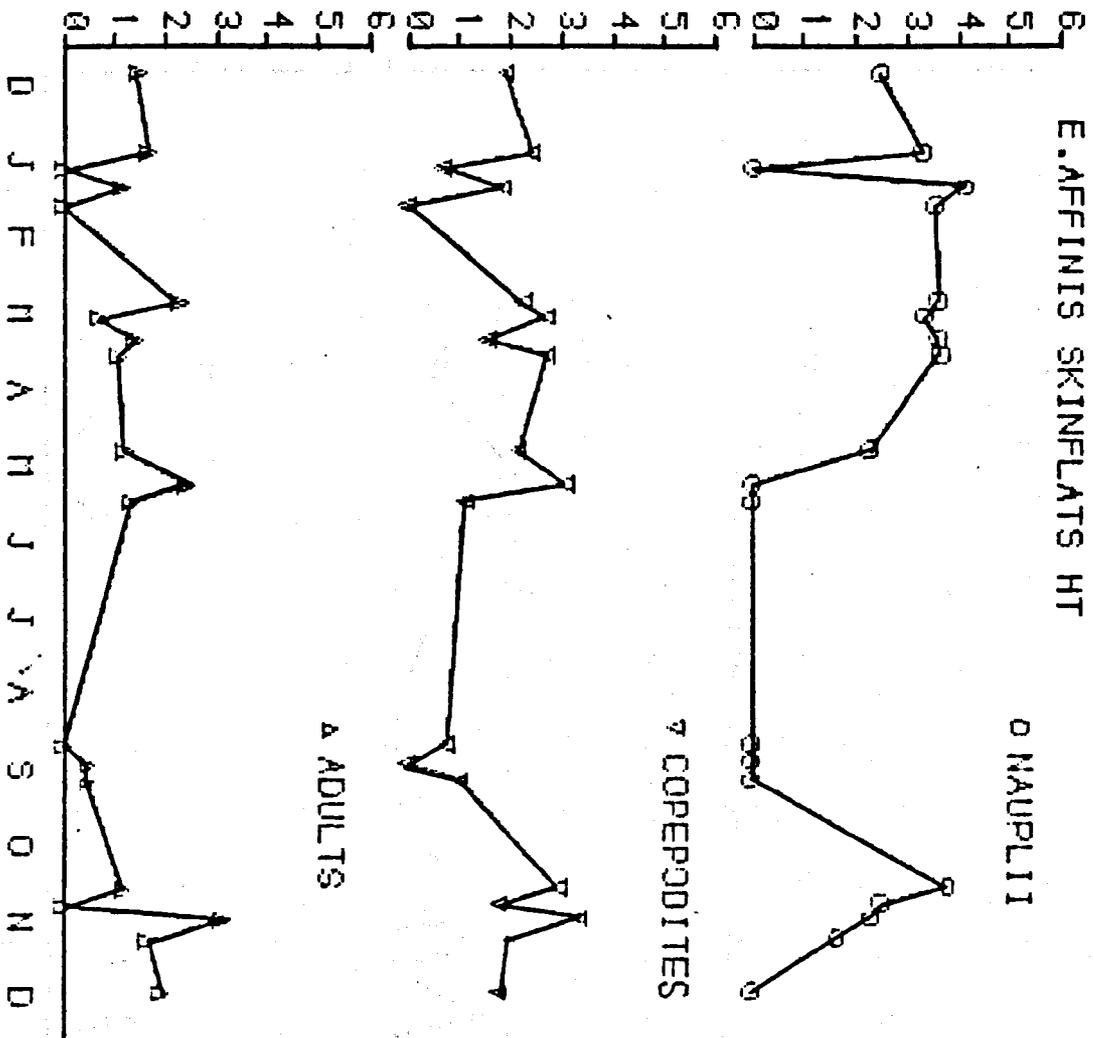


Fig. 1.21 Abundance of E. affinis;Skinflats high tide

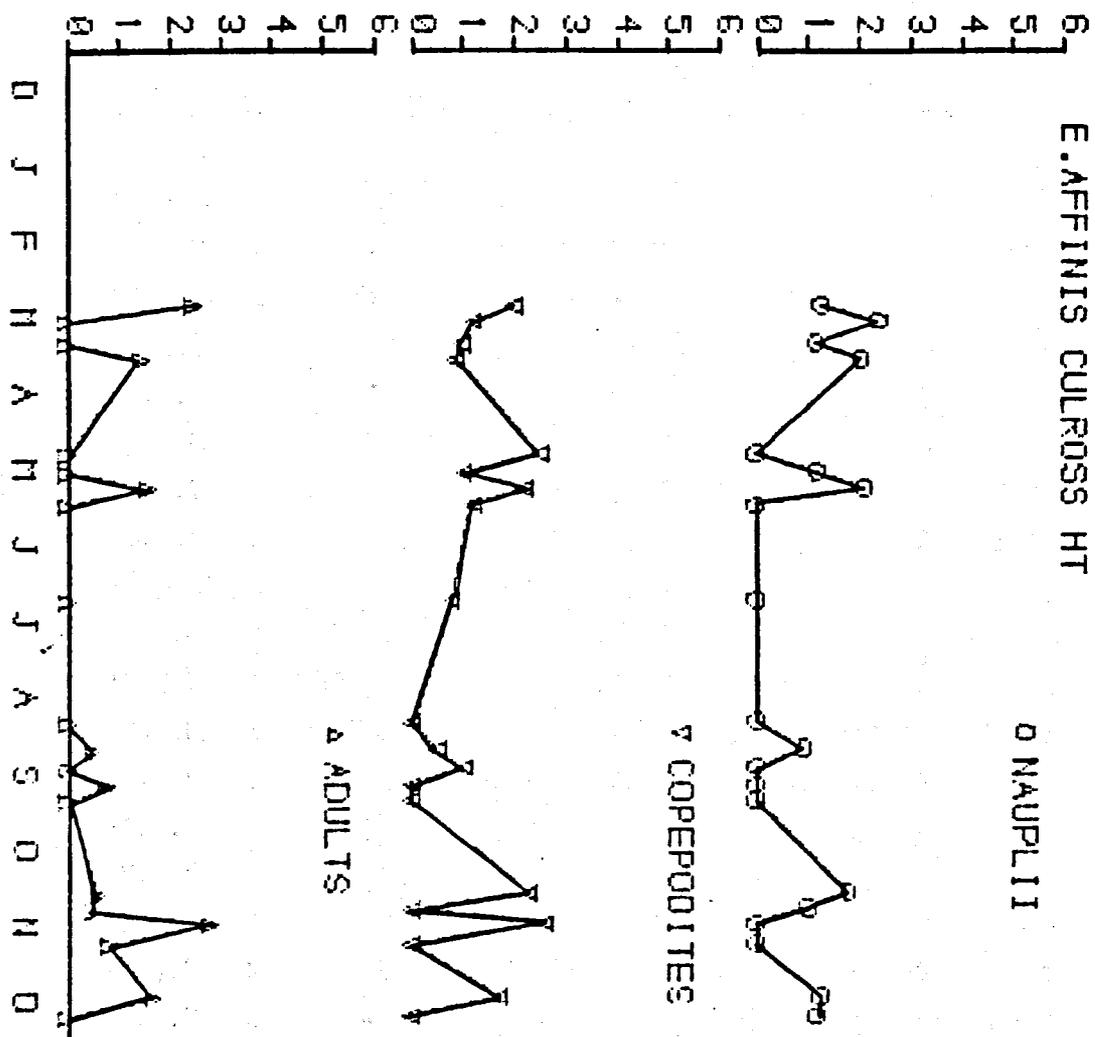


Fig. 1.22 Abundance of E. affinis:Culross high tide

Table 1.8 Annual variation in mean abundance of E.affinis (all stages, nos. per cubic metre) at Fallin, S.Alloa and Dunmore on high and low tides, 1982

Date	Tide	Fallin		S.Alloa		Dunmore		Kincardine	
		HT	LT	HT	LT	HT	LT	HT	LT
11.12.81	S	14671	-	8873	-	1235	-	45	-
15.12.81	N	-	291	4950	873	2709	261	351	597
12.1.82	S	6822	114	14517	1397	1975	6530	518	1674
19.1.82	N	122	36	2223	90	1007	257	32	492
27.1.82	S	186	0	4178	260	771	1174	57	133
3.2.82	N	727	26	14145	599	399	1550	418	114
11.3.82	S	59	32	3976	51	2615	1793	4153	382
18.3.82	N	82	88	3554	465	1658	6103	573	704
26.3.82	S	27205	307	4981	54536	1253	12013	1921	4889
2.4.82	N	24279	76	14108	6868	12258	179796	361	336
10.5.82	S	139503	954	17682	18609	8880	358	390	1263
17.5.82	N	98519	59888	63385	16629	43620	26976	5302	1843
24.5.82	S	266032	5499	49388	96280	10999	121389	1129	19922
31.5.82	N	250741	182561	72280	70390	6462	95063	908	7499
8.7.82	S	25921	-	45348	-	954	-	42	-
6.9.82	S	71	6	201	65	0	48	0	-
13.9.82	N	17	11	128	45	39	312	2	31
20.9.82	S	-	69	1642	128	18	358	-	400
27.9.82	N	42	23	333	38	19	376	10	30
3.11.82	S	499	54	3296	32	1056	54	1341	-
9.11.82	N	71	8	682	31	6815	3977	97	269
16.11.82	S	-	176	7085	261	2440	10088	26	639
22.11.82	N	-	-	3193	14	1350	96	182	280
15.12.82	S	-	-	1541	1594	998	2116	419	169
23.12.82	N	51	0	2206	51	1470	422	288	1670

Kincardine was 19922 m⁻³ on the same date.

At Fallin, high tide abundances exceeded low tide abundances throughout the year, while at S.Alloa, Dunmore and Kincardine low tide abundances generally exceeded high tide abundances.

At all stations, abundance declined dramatically between July and September (Figs.1.17-1.22), recovering (least notably at Fallin) in November.

The spring population maximum coincided with the period of minimum size noted above, and the late summer decline with the period of maximum size.

Naupliar, copepodite and adult abundances were plotted on log scales to facilitate comparisons of trends between these age groups and between stations (Figs.1.17-1.22). The same seasonal trend was evident at all stations, but more striking at each station was the extent to which the age groups reflected the same fluctuations. The fluctuations were, however, only comparable in the broadest sense between stations. The figures suggest that sampling variability and/or small-scale spatial variability contribute an important element of noise to abundance estimates.

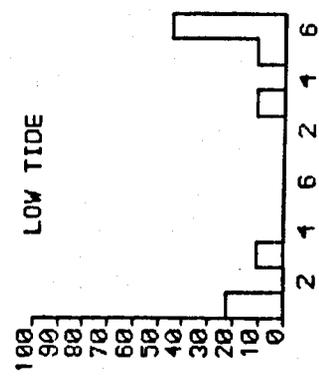
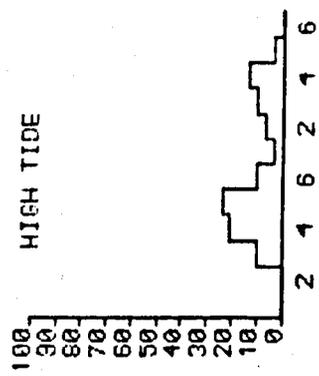
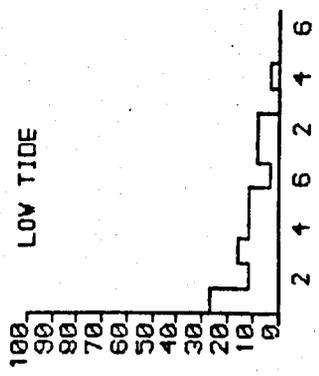
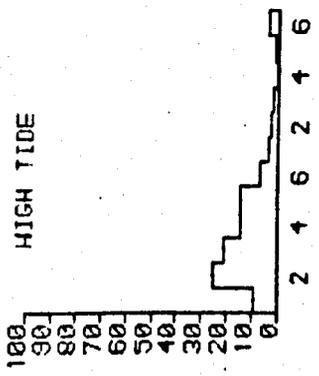
Age structure

The percentage distribution of stages within samples was calculated for Fallin, Dunmore and S.Alloa (Figs.1.23-1.25). Whilst there was some consistency between S.Alloa and Dunmore age structures prior to April 1982 (Figs.1.24,1.25), there was no evidence of either consistent age structure over short time periods or of systematic change in age structure on a seasonal basis. It is thus unlikely that structure was determined by overall synchrony of

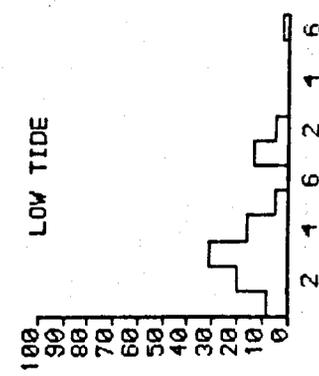
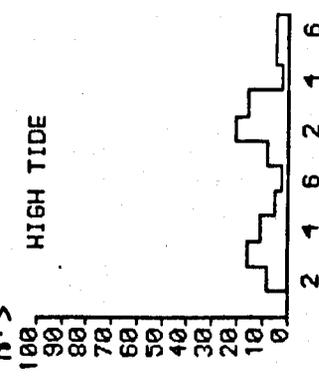
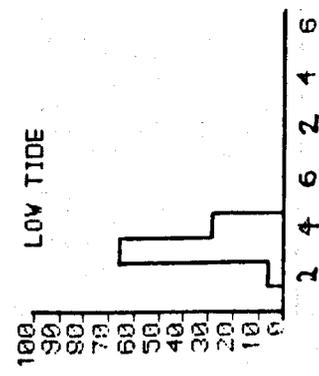
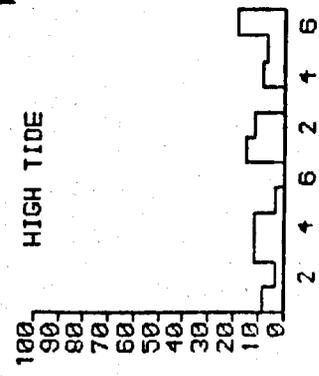
reproduction in the population (which might have led to the development of identifiable cohorts) or that there was a strong influence of age- or density-dependent mortality in a continuously-reproducing population (which might have led to a constant decline in relative abundance with age). It is likely that reproductive processes are patch-dependent and that the sampling method integrates the information from several patches in an uncontrolled manner.

The stage-frequency histograms did, however, emphasise the presence of nauplii in at least some samples on all sampling dates, showing that E.affinis breeds throughout the year.

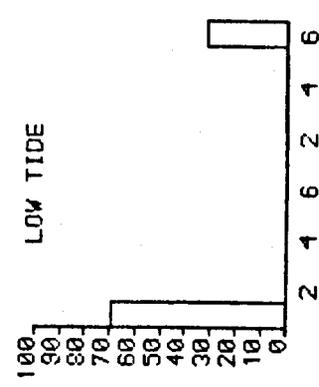
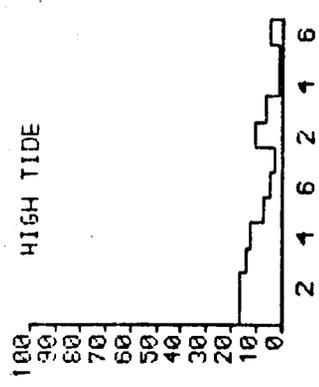
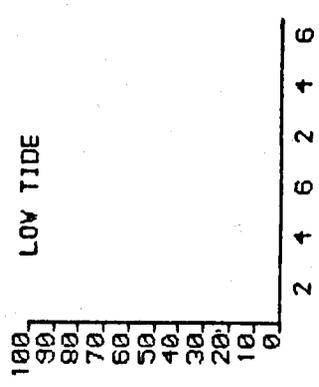
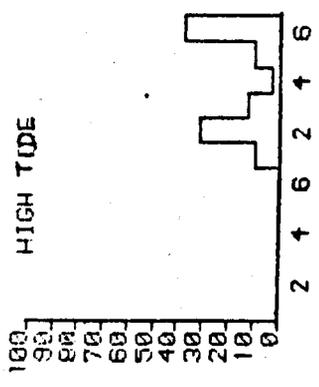
FA 12.1/19.1



FA 11.3/18.3



FA 27.1/3.2



FA 26.3/2.4

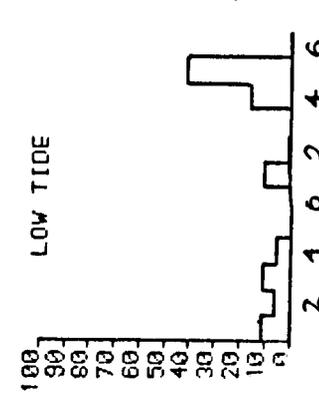
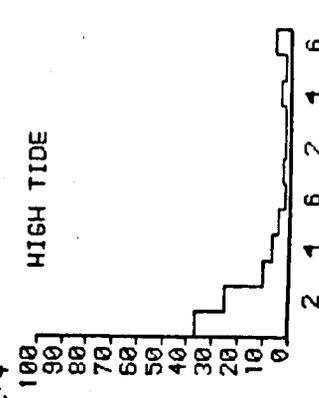
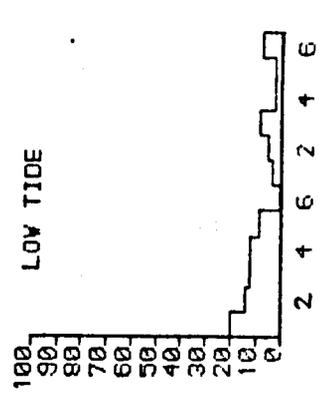
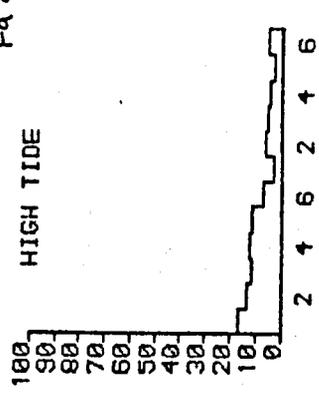
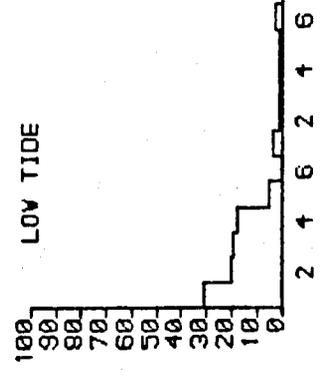
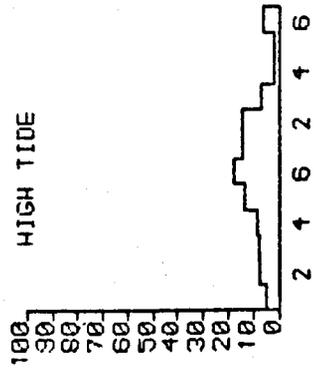
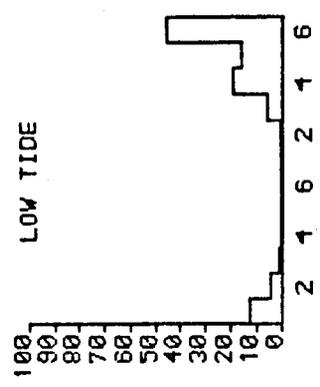
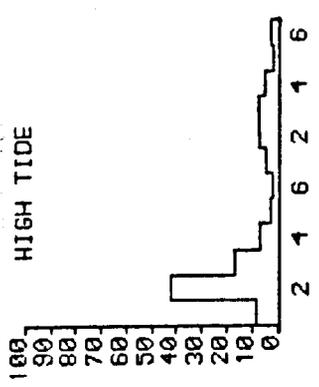
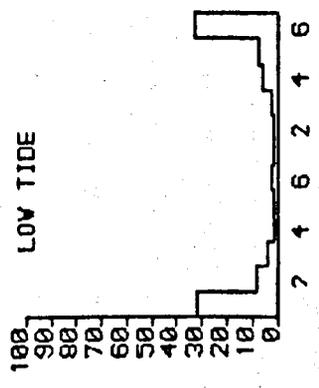
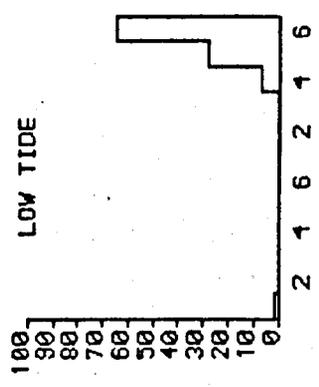
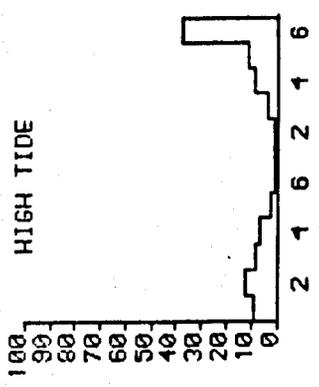


Fig. 1.23 a Stage-frequency distribution; Fall in

FA 24.5/31.5



FA 18.5/17.5



FA 8.7/26.8

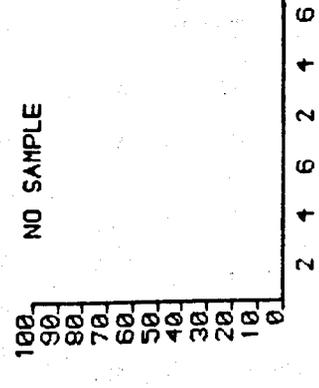
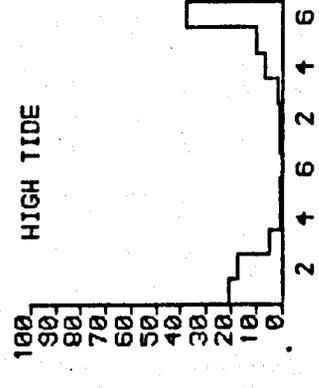
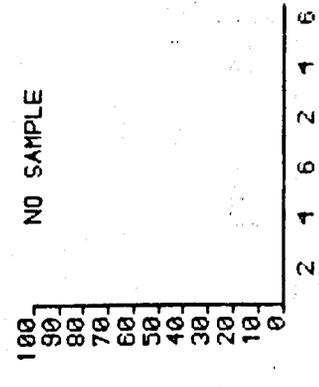
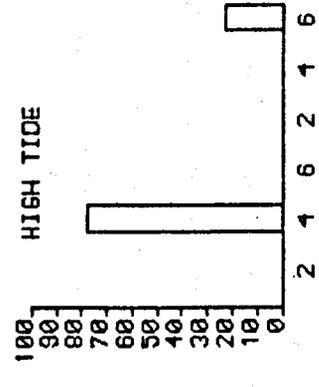
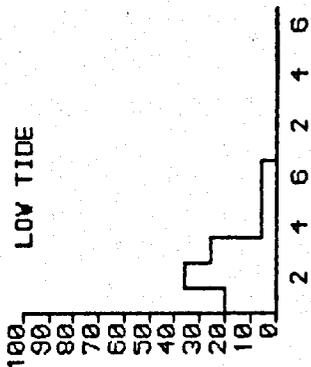
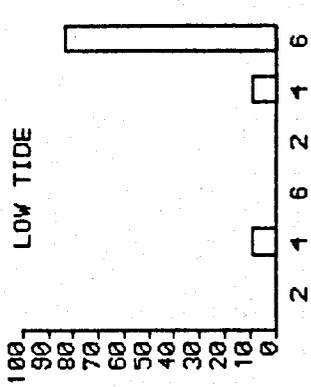
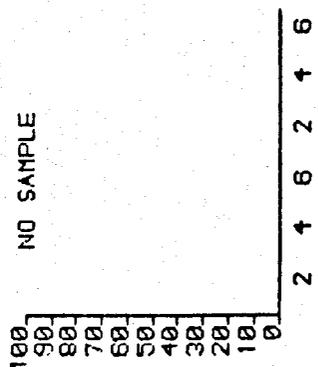
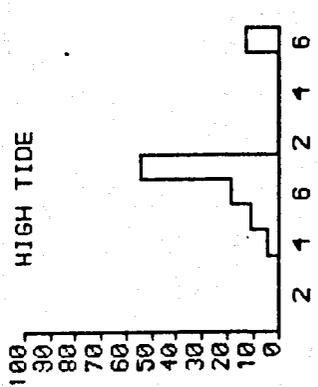
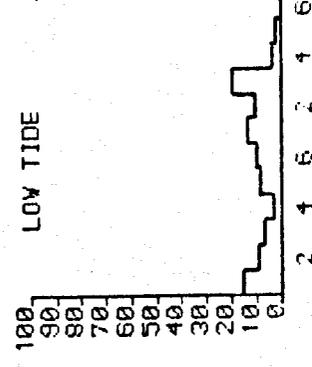
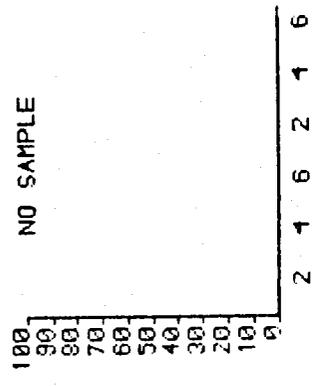
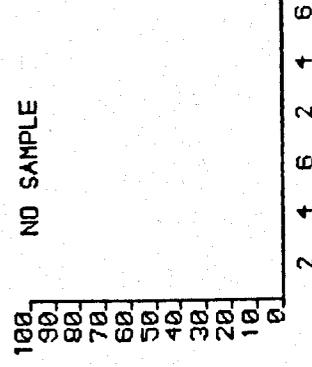
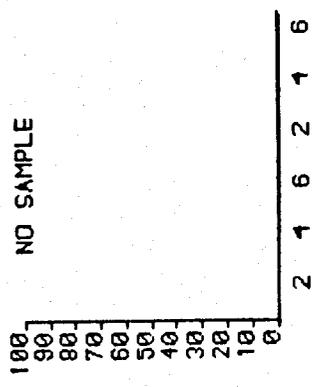


Fig. 1.23 b Stage-frequency distribution: Fall in

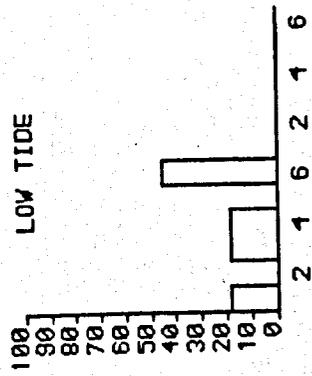
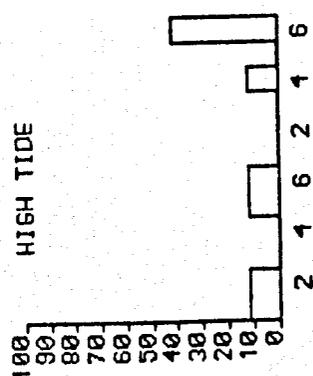
FA 20.9/27.9



FA 16.11/22.11



FA 6.9/13.9



FA 3.11/9.11

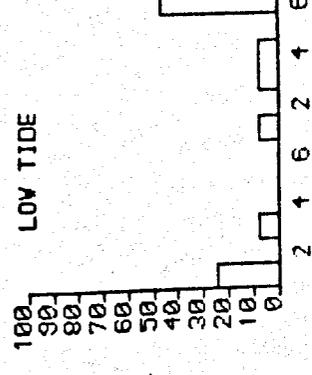
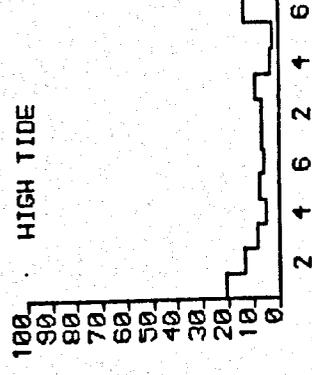
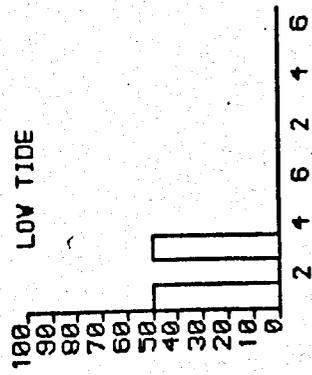
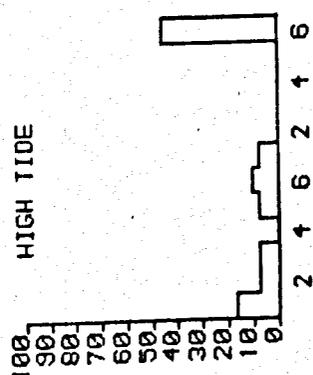
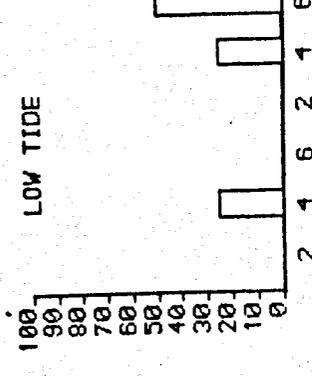
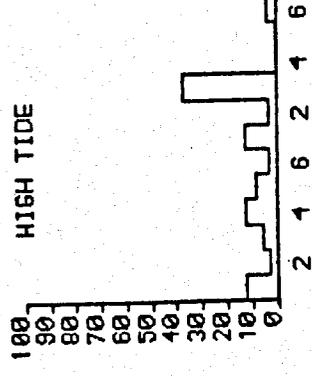
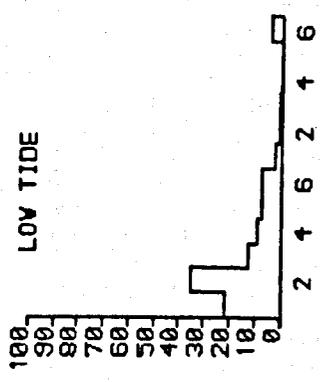
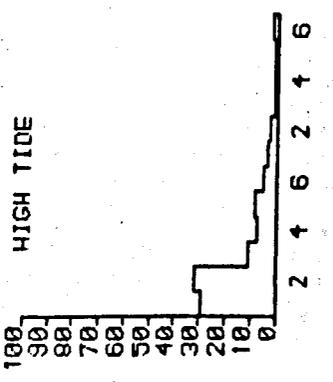
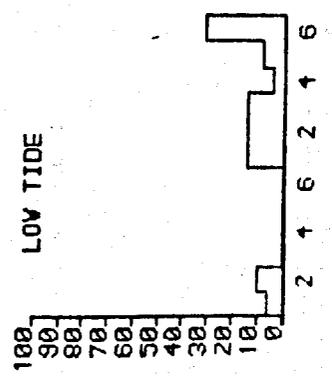
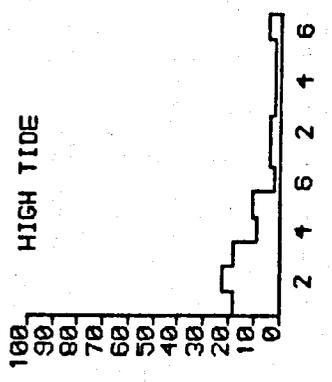


Fig. 1.23 c Stage-frequency distribution:Fallin

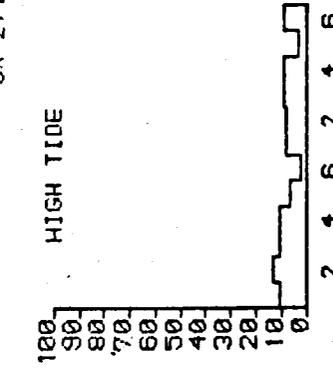
SA 12.1/19.1



SA 11.3/18.3



SA 27.1/3.2



SA 25.3/2.4

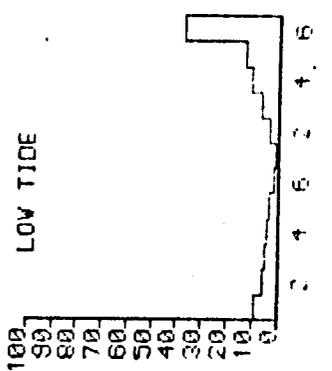
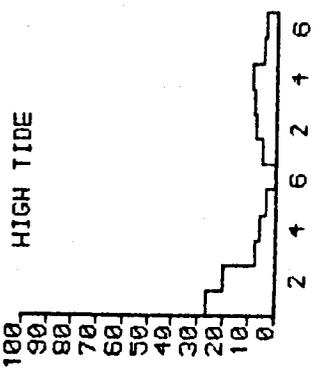
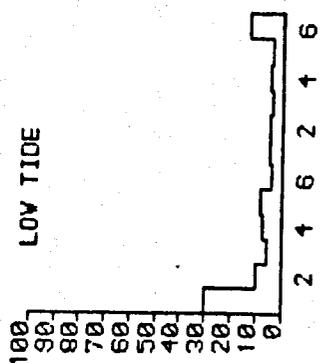
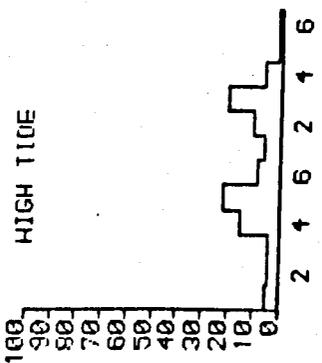
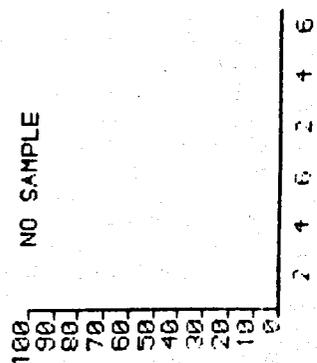
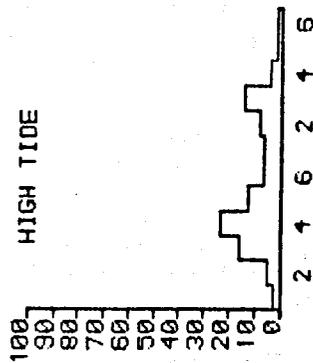


Fig. 1.24 a Stage-frequency distribution:South Alloa

SA 10.5/17.5



SA 8.7/25.8



SA 24.5/31.5

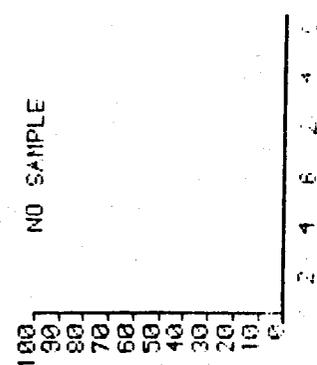
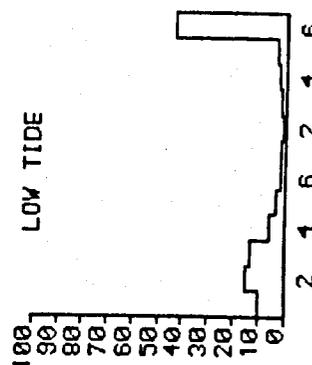
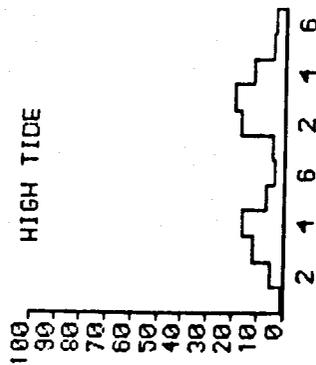
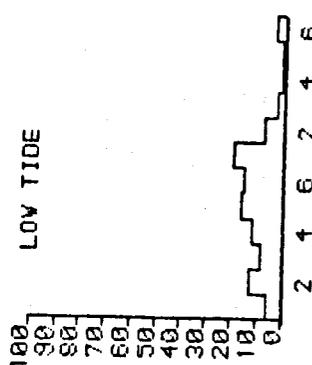
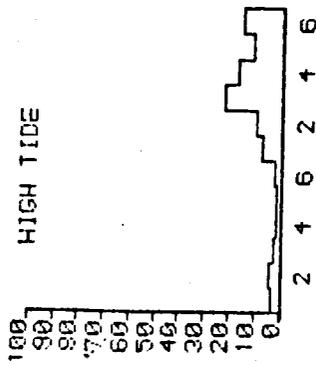
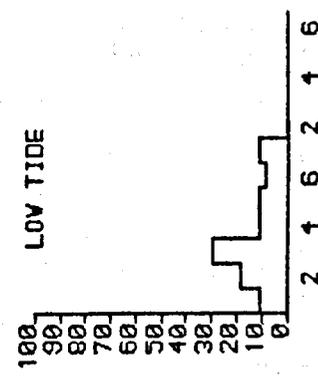
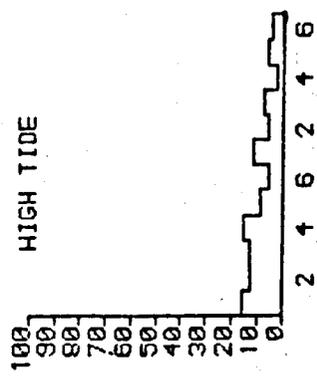
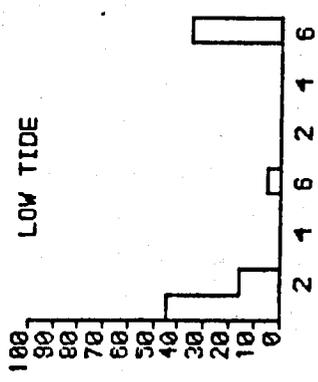
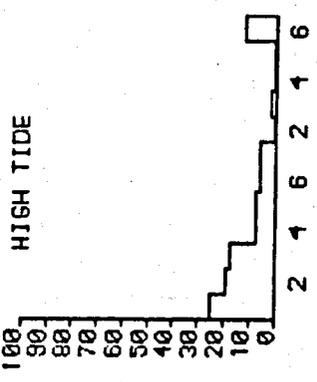
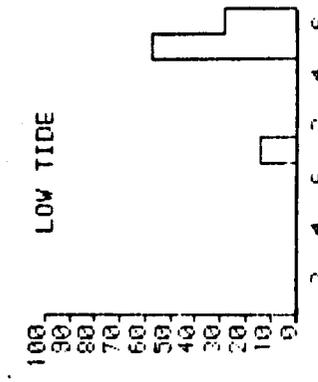


Fig. 1.24 b Stage-frequency distribution; South Alloa .

SA 20.9/27.9



SA 16.11/22.11



SA 3.11/9.11

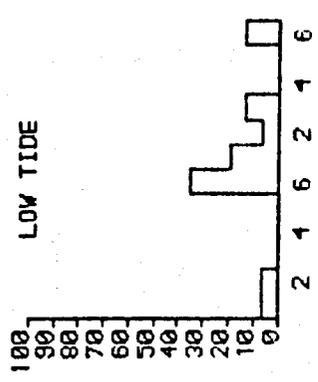
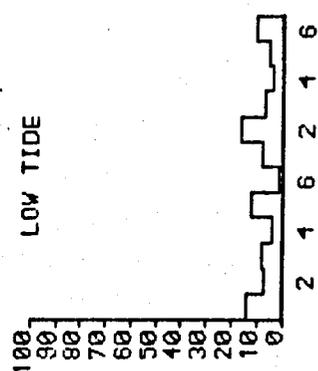
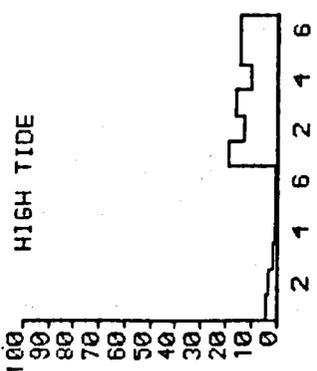
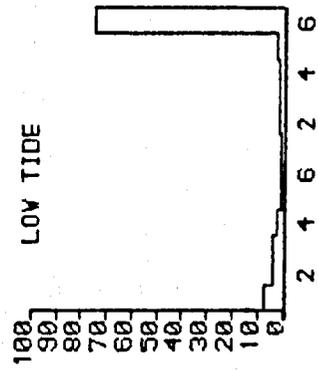
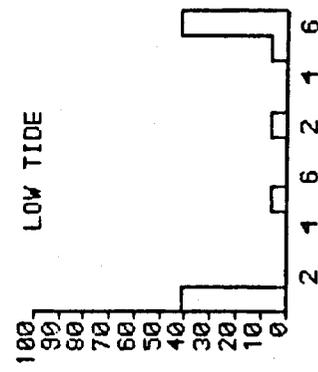
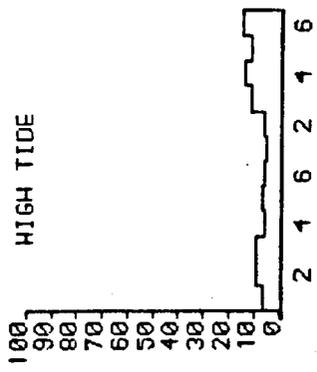


Fig. 1.24 c Stage-frequency distribution, South Alloa

SA 15.12/23.12



SA 11.12/18.12

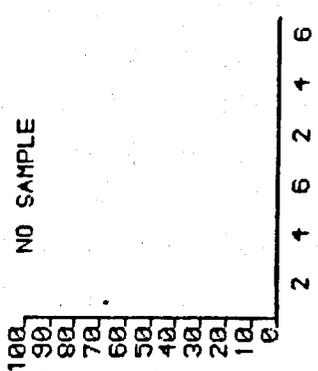
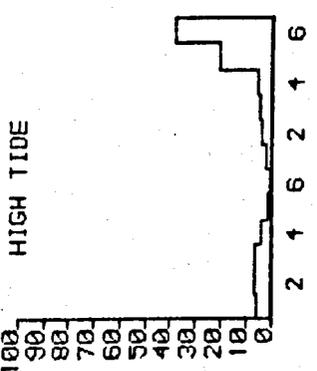
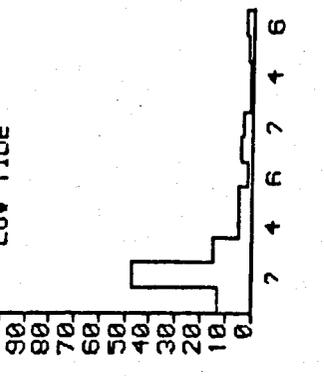
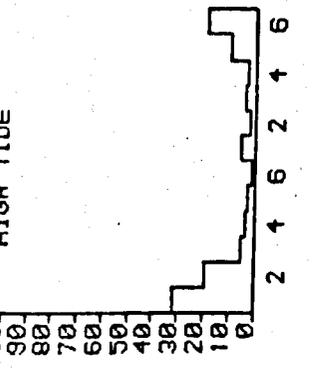
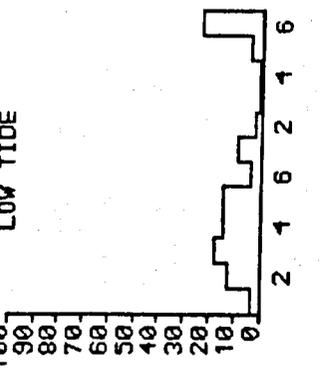
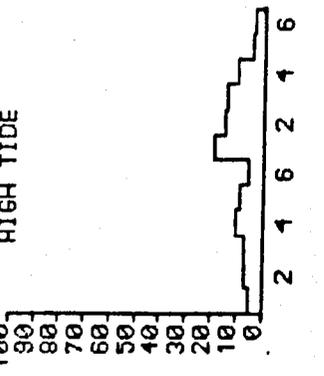
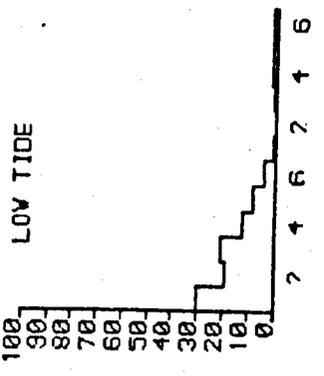
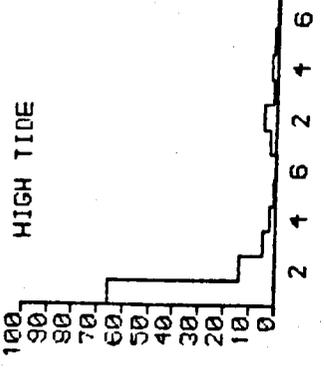
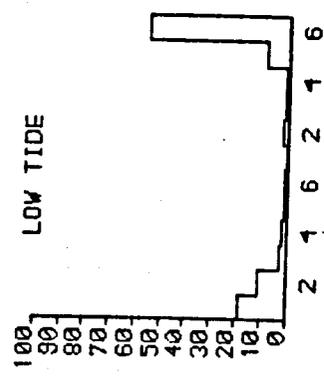
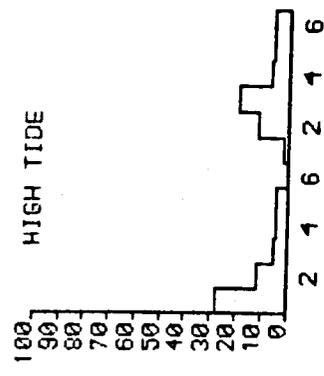
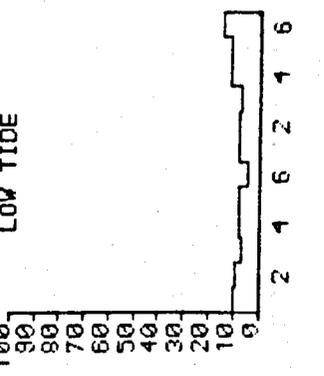
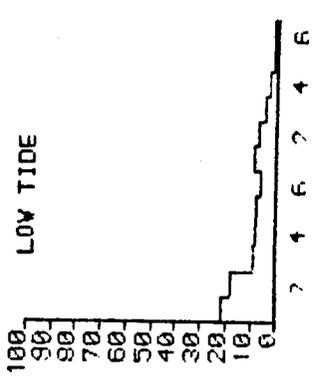
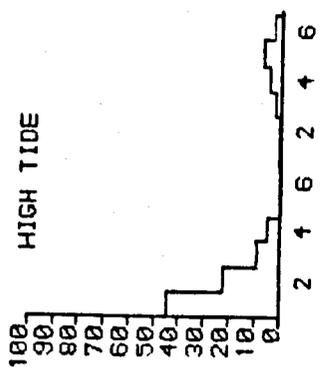
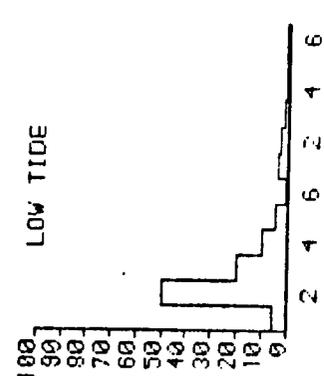
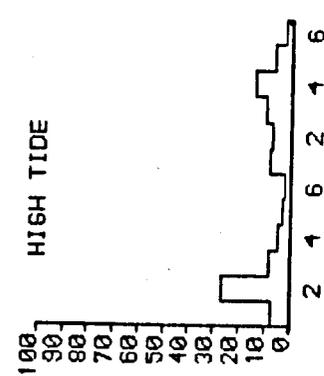


Fig. 1.24 d Stage-frequency distribution:South Alloa

DU 27.1/3.2



DU 26.3/2.4



DU 11.3/18.3

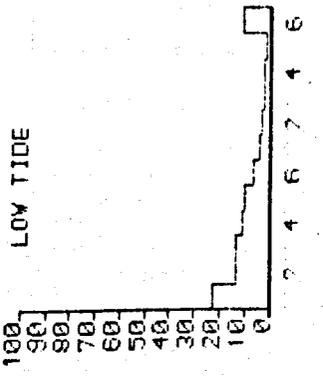
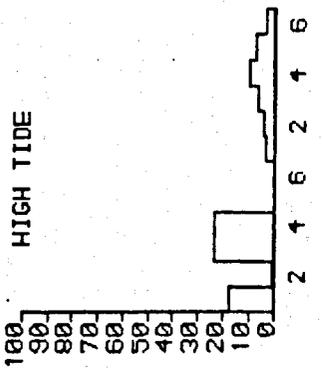
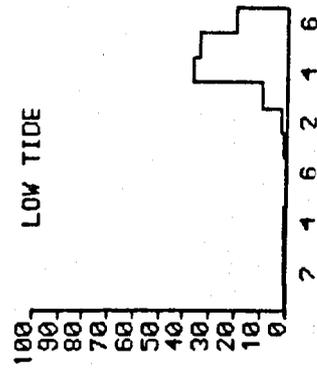
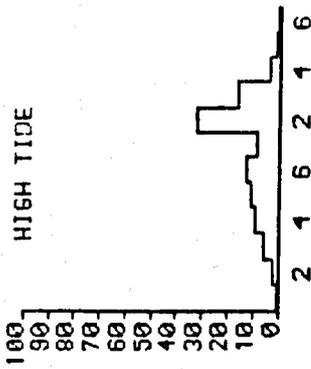
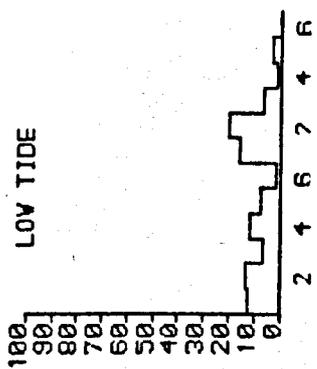
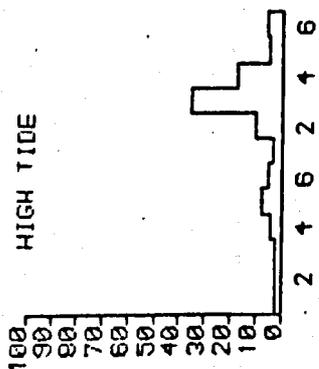
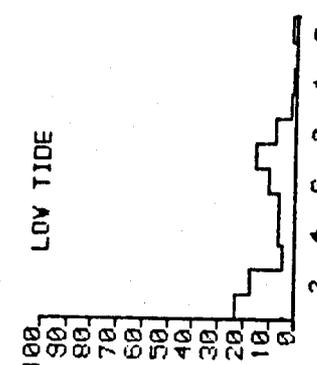
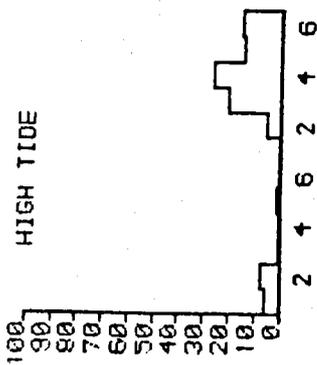


Fig. 1.25 a Stage-frequency distribution: Dummore

DU 10.5/17.5



DU 24.5/31.5



DU 8.7/26.8

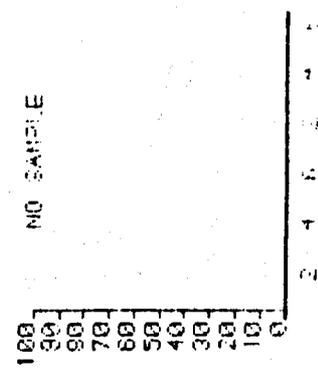
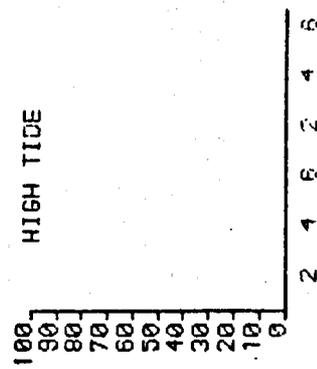
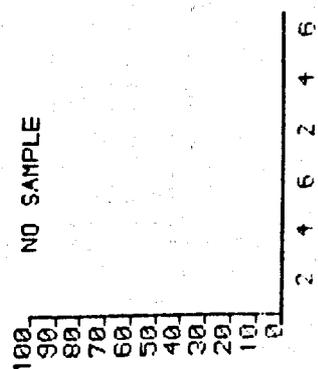
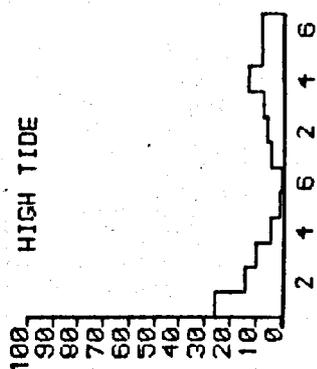
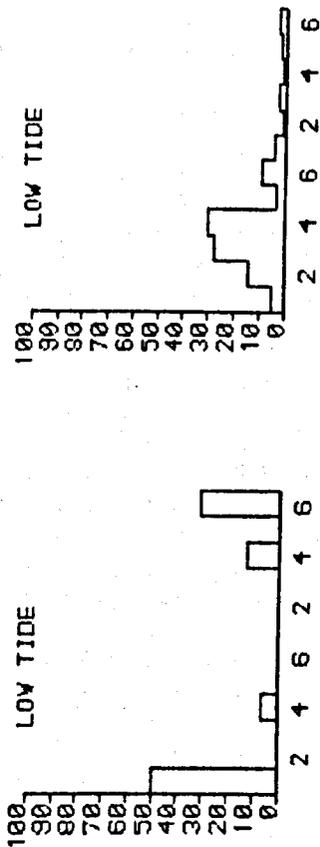
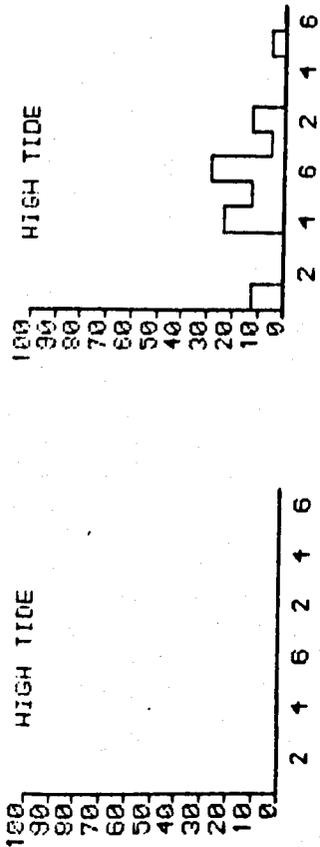
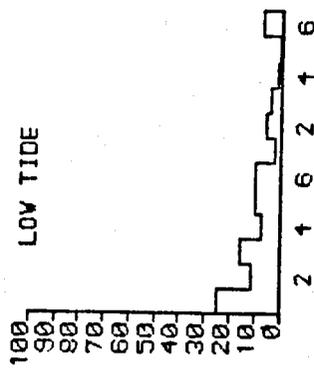
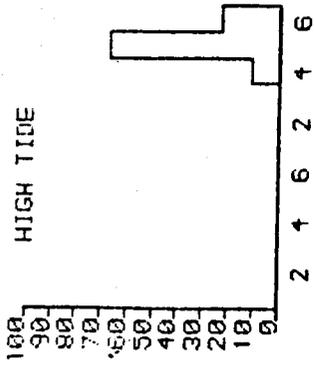


Fig. 1.25 b Stage-frequency distribution: Dunmore

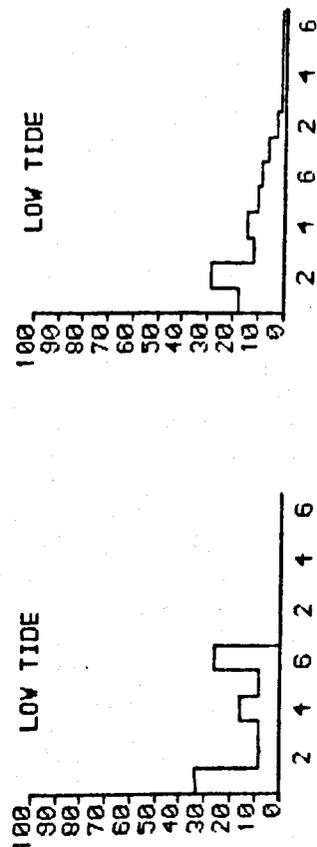
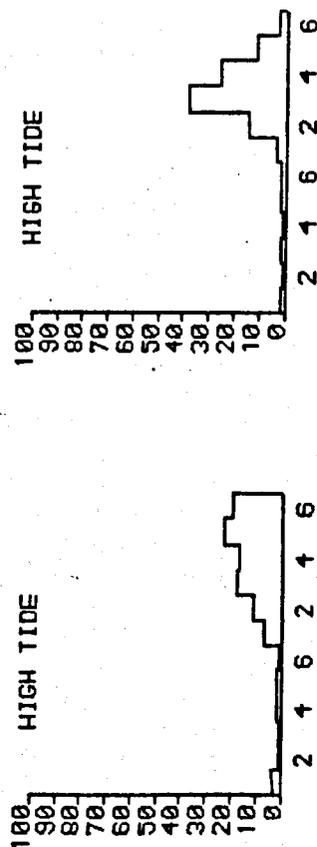
DU 6.5/13.9



DU 20.9/27.9



DU 3.11/9.11



DU 16.11/22.11

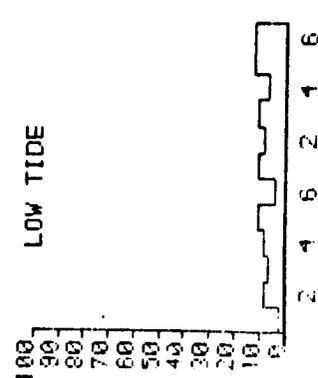
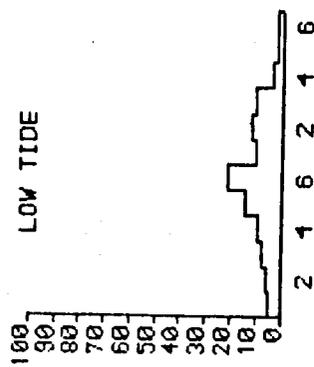
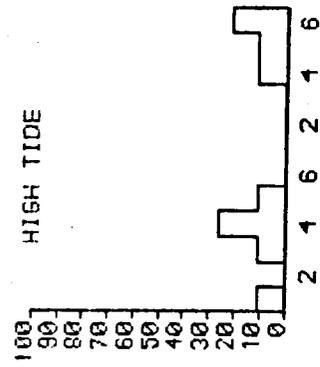
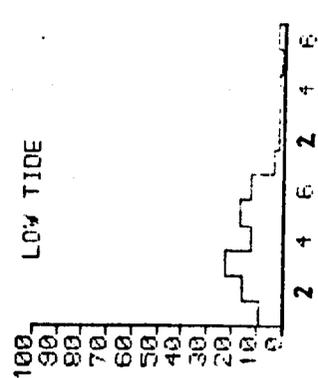
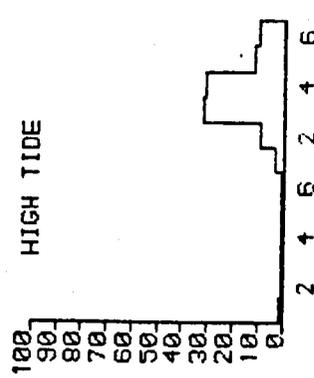
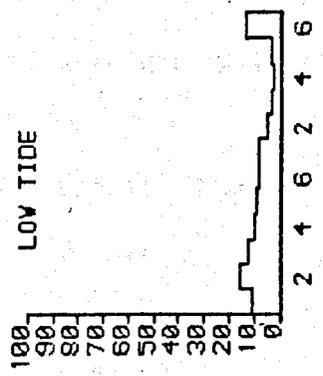
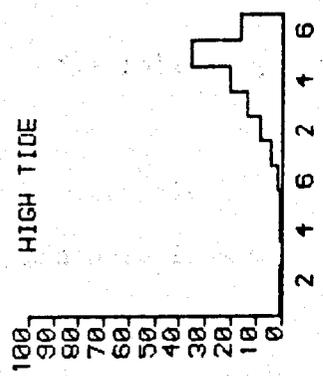
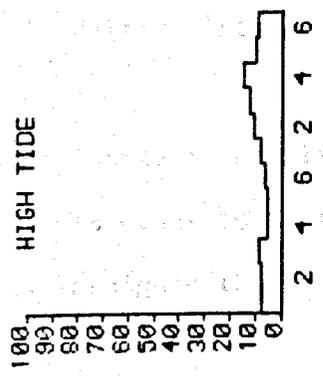


Fig. 1.25 c Stage-frequency distribution;Dunmore

DU 15.12/23.12



DU 11.12/18.12

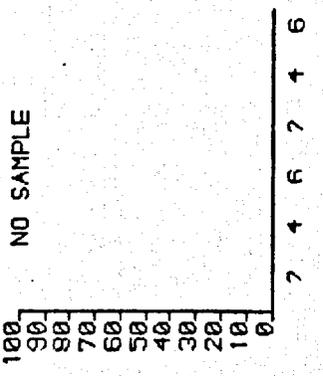
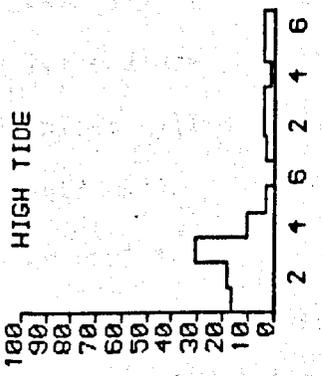
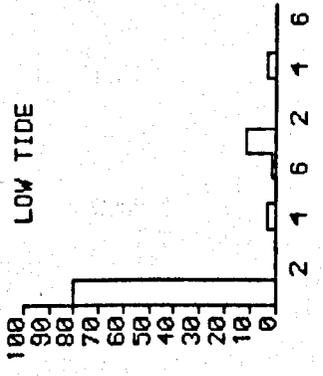
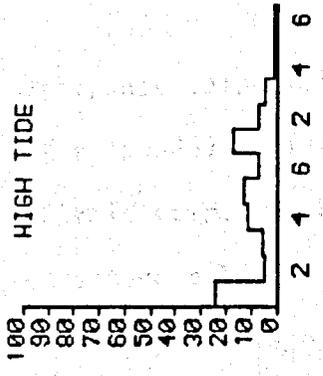


Fig. 1.25 d Stage-frequency distribution; Dunmore

Multivariate analysis of field survey data

Sample identifiers

In order to avoid confusion with S.Alloa, Skinflats has been assigned the identifier G (for Grangemouth, an adjacent town).

Environmental variables

The following variables were used in analyses:

Variable	Shorthand identifier	Transformation
Distance from upper tidal limit	Dist	Log10
Tidal state (H,N etc)	Tide	Dummy 4-state variable
Date	Date	None, represented as decimal month
Inorganic component of suspended solids	Inor	Log10
Organic component of suspended solids	Org	Log10
Organic percentage of suspended solids	%org	$\arcsin/\sqrt{\log_{10} X+1}$ (x as proportion)
Salinity	Sal	None
Temperature	Temp	None
Chlorophyll a	Chl a	Log10
Acid Ratio	AR	Log10
Phaeopigments	Phae	Log10
Freshwater discharge at upper tidal limit	Disch	None

Data on freshwater discharge was obtained from the Forth River Purification Board (FRPB 1983).

Suspended solids values were recorded in mg/l, and Chla in ug/l.

The entire 1981/1982 data set was subdivided into logical categories for analysis. Subsets were extracted corresponding to station, date(sampling cycle) and tidal state.

Station and date categories were subjected to DCA,TS and MDA analysis. Similar analyses were conducted for tidal state, but for tidal groups a further step was taken by projecting the significant environmental variables onto the ordination space defined by the first two discriminant functions in order to illustrate their relative magnitude and direction of influence in discriminating between groups. Accordingly, less emphasis will be placed on comparisons of DCA and TS analyses for tidal groups.

Twinspan

Analyses have been taken to the second (four groups) or third (eight groups) level of division. The convention has been adopted of referring to the groups thus defined in numerical sequence from left to right on two-way ordered tables and top to bottom on the corresponding dendrograms. No correspondence between TS groups of similar number in different categories is implied.

On each dendrogram, the indicator species defined by Twinspan at each division have been shown using the shorthand identifiers given in Table 1.4.

Environmental data

A certain number of samples have been excluded from DCA correlations with environmental data, and from MDA analysis, due to the incompleteness of the environmental data set.

Correlations between DCA axis 1 and axis 2 sample scores and environmental variables are summarised for the various sample categories in Tables 1.12-1.14.

For MDA, variables with a significant univariate between-groups F-ratio for each sample category are shown in Table 1.10. Variables with the strongest pooled between-groups correlations with scores on the first two discriminant functions are given in Table 1.11a, with the sign of the correlation indicated. The percentage of variance accounted for by the first two functions, and the percentage of samples correctly reclassified by the linear discriminant solution, are given in Table 1.11b. For all MDA analyses, samples were classified on the basis of prior probability; that is, they were assigned a probability of occurring in a given group equal to the relative size of the group. In addition to the transformations described above, all variables were standardised before being entered into the analysis, to remove any possible undue influence arising from a difference in scale between variables.

Taxa included in analysis

Preliminary trials indicated that the degree of association between the three original Eurytemora categories was such that combining them into one category produced identical results.

Ambiguous categories such as unidentified copepod nauplii and Acartia juveniles were excluded from the analysis and some rarer categories such as aphroditid larvae and Acartia discaudata were included when it became apparent that the downweighting option invoked in both TS and MDA analyses operated effectively on these taxa.

Table 10 Variables with a significant univariate within-group to between-group F-ratio ($p < 0.05$) ; groups derived by Twinspan classification of samples within logical categories

Category	Variable											
	Dist	Tide	Date	Disch	Inorg	Org	%org	Chl a	Phaeo	AR	Sal	Temp
Gp1			-	-								
Gp2	*		-	-	*						*	*
Gp3	*	*	-	-			*		*	*	*	
Gp4	*	*	-	-			*		*	*	*	
Gp7	*	*	-	-	*	*	*		*	*	*	*
Gp8	*	*	-	-	*	*			*		*	
Gp9			-	-								
FA	-			*		*	*	*	*			*
SA	-		*	*			*			*	*	*
DU	-	*	*	*				*		*	*	*
KI	-		*	*				*		*	*	*
SK	-		*	*								*
CU	-		*	*							*	*
High	*	-	*	*			*	*		*	*	*
Low	*	-	*	*			*	*	*		*	*
Spring	*	-	*	*	*	*	*	*	*	*	*	*
Neap	*	-	*	*	*	*	*	*	*	*	*	*
HS	*	-	*	*			*	*		*	*	*
LS	*	-	*				*	*		*	*	*
HN	*	-	*	*			*	*		*	*	*
LN	*	-		*				*			*	*

Table 1.1A Summary of structure matrices generated by Multiple Discriminant Analysis: Variables with highest pooled within-group correlations with discriminant function scores and the sign of the correlation

Tides			Dates			Stations		
	Func 1	Func 2		Func 1	Func 2		Func 1	Func 2
H	Sal + Dist +	Date +				FA	Temp + Phae +	Discht+ %org + Date -
L	Dist + Sal +	Date +	GP2	Dist +	Temp + Sal + Inor +			
Sp	Sal +	Chl a-	GP3	Sal + Dist+ Tidet+ %org+	AR -	SA	Sal + Disch- %org -	Date - Chl a- AR -
Ne	Sal + Dist +	Date +						
HS		Discht+ Date + Temp-	GP4	Sal +	Dist + Tide -	DU	Temp + AR + Chl at Disch-	Sal + Tide + Date -
LS	Chl a- AR - Temp -	Dist + Date + Sal + %org-	GP7	Sal + Dist+	Inor - Phae - AR +			
				Tidet+		SK		Date + Discht+
HN	Sal + Dist+	Date+ Discht+	GP8	Sal + Dist+	Phae + Inor +	CU	Date +	Temp- Discht+ Sal -
LN	Sal + Dist+ Temp+	Chl at Discht+ Date+						

Table 1-11b Multiple Discriminant Analysis: Percent variance accounted for by first two discriminant functions, and percentage successful reclassification of samples

Category	Variance explained			Reclassification
	Func 1	Func 2	Total	
All samples	51.4	31.3	82.7	70.3
High tide	50.6	35.1	85.7	71.1
Low tide	43.2	28.5	71.7	75.0
Spring tide	46.2	39.0	85.2	77.3
Neap tide	54.8	25.0	79.8	72.7
High neap	56.0	20.2	76.2	79.6
Low neap	75.0	18.6	93.6	88.6
High spring	83.8	7.8	91.6	85.5
Low spring	69.0	18.8	87.8	90.9
Fallin	63.4	26.5	89.9	90.3
S.Alloa	58.3	35.6	93.9	85.5
Dunmore	50.1	34.6	84.7	81.1
Kincardine	49.9	41.2	91.1	91.2
Skinflats	77.1	16.6	93.7	100.0
Culross	90.0	5.8	95.8	100.0
Gp 2	64.1	34.0	98.1	100.0
Gp 3	59.3	25.6	84.9	85.0
Gp 4	96.8	1.7	98.5	86.2
Gp 7	89.4	8.1	97.5	91.7
Gp 8	89.9	6.8	96.7	97.2
Gp 9	83.9	13.6	97.5	100.0

Table 1-12 Correlation between DCA first and second axis sample scores and log-transformed environmental variables: Samples categorised by tidal state (Significance Levels: * = 0.05, ** = 0.01, *** = 0.001)

Variable	Tidal state															
	High		Low		Spring		Neap		HS		LS		HN		LN	
	A1	A2	A1	A2	A1	A2	A1	A2	A1	A2	A1	A2	A1	A2	A1	A2
Dist	***	*	*		***	*	***				*		***		**	
Tide	-----															
Date	*			**		*		**	**			***		**		**
Disch			**		*		**	**	*		**		**	**	*	
%org	*		**		***		**		*		***					
Sal	***	*	**		***	**	***		**	**			***		**	
Temp	***		**		***		**		**		**		**		**	
Inor					***											
Org					**											
Chl a	*					***			*			***				
AR	*			*	**				*			***				
Phaeo					**											

Table 1.13 Correlation between DCA first and second axis sample scores and log-transformed environmental variables: Samples categorised by Station Significance levels as Table 1.12

Variable	Station											
	Fallin		S.Alloa		Dunmore		Kincardine		Skinflats		Culross	
	A1	A2	A1	A2	A1	A2	A1	A2	A1	A2	A1	A2
Dist	---	---	---	---	---	---	---	---	---	---	---	---
Tide			**		**							
Date	*		*		*		**		*	*	*	*
Disch		**						**	**		**	
%org												
Sal			**	*	**	*	*					
Temp	**		**		**		**				**	
Inor	*											
Org	*											
Chl a	**		**		**		**			**		
AR			*		**		**			*		*
Phaeo	**											

Table 1.14 Correlation between DCA first and second axis sample scores and log-transformed environmental variables: Samples categorised by Date Significance levels as Table 1.12

Variable	Sample group (chronological order)															
	Gp1		Gp2		Gp3		Gp4		Gp5		Gp7		Gp8		Gp9	
	A1	A2	A1	A2	A1	A2	A1	A2	A1	A2	A1	A2	A1	A2	A1	A2
Dist	**		**		***		**		***		***		***		**	
Tide					**		**				**		**			
Date	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
Disch																
%org					*		**		**	**	**	**	**	**	**	**
Sal	**		**		***		***		***		***		***		**	
Temp	*		*		*				*	*	*	*	*	*	*	*
Inor			**			*	*		*		**		**			
Org			**			*			*		*		*			
Chl a									*		*		*			
AR							*		***		***		***			
Phaeo			*	**			*		*		**		**			

1. Samples categorised by station

Culross

There were a total of 20 samples in this group.

DCA analysis indicated that axes 1 and 2 were of equal length, a value of 250 implying an approximately 75% turnover in species along each axis (Gauch and Whittaker, 1981)(Fig.1.26b). Date was significantly correlated with both axes ($p < 0.05$), while Temp and Disch were highly correlated ($p < 0.01$) with axis 1. AR was correlated ($p < 0.05$) with axis 2 only (Table 1.13). TS analysis was carried to three levels of division, but only 5 groups could be derived (Fig.1.26a, Table 1.15). The primary division was characterised by the indicators Pseudocalanus and Rotifera on one side (winter/spring) and Polydora larvae and cirripede larvae on the other (summer/autumn).

At the second level, May samples were indicated by terebellid, nereid and cirripede larvae, while winter samples were characterised by a tight Maranzelleria group and two further groups dominated by Acartia spp. and Pseudocalanus. Oithona and Eurytemora were present in most samples.

Date, Disch, Sal, Temp had significant univariate F-ratios (Table 1.10). Analysis revealed that Date was positively associated with Function 1 (Table 1.11a), while the remaining variables were negatively associated with Function 2. The groups were very well

Table 1.15 Twinspan classification of Culcross samples

CU

		1111	1112		111	
		1234	1567	4890	5676	9023
26	ROTI SPEC	32--	32--	322--	----	000
29	MARA WIFE	3232	----	----	----	000
30	MARA TRUC	3-1-	----	----	----	000
31	MARA EGGS	4-2-	----	----	----	000
8	ACAR CLAU	-1--	12--	----	----	001
13	ACAR DISC	----	3--	----	----	001
16	PSEU ELON	--1-	1323	-2112	----	001
23	SAGI ELEG	1----	11--	----	----	001
9	ACAR LONG	----	22-1	----	1-11	010
24	OIKO DIOI	----	32--	----	--2	010
5	EURY AFFI	3323	2324	-132	3232	1-11
12	ACAR INER	2----	221--	----	2-2--	0110
19	CALA HELG	11--	----	----	1----	0110
20	TEMO LONG	211-	1211	-1--	2-11	-1-
17	OITH SIMI	2-2-	2322	-221	3-2-	1212
27	HARP SPEC	2322	3232	1332	3323	2123
10	ACAR TONS	----	12-1	----	----	-112
32	LITT CAPS	4242	11--	--3-	4244	3--2
40	CIRR NAUP	3222	3221	123-	4333	4434
18	CENT HAMA	1----	----	----	2--1	1----
28	POLY CILI	----	1--	1111	4332	2-22
33	LITT VELI	-12-	----	----	231-	1----
37	TERE LARV	1----	----	----	3122	----
38	NERE LARV	----	----	----	11--	----
39	CIRR CYPR	----	2--	----	3211	11-2
42	NUDI JUVE	----	----	----	22--	----
41	BIVA LARV	----	----	----	1----	1111
		0000	0000	0000	1111	1111
		0000	1111	1111	0000	1111
			0000	1111		

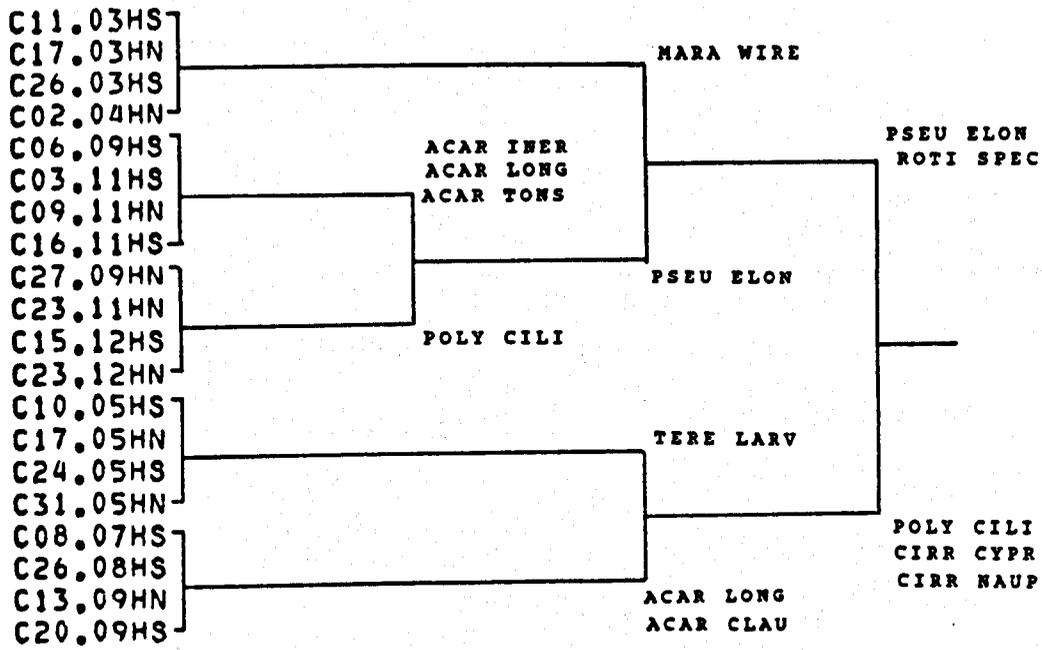


Figure 1.26 a

Dendrogram of Culross samples classified by Twinspan. Indicator species for each division shown.

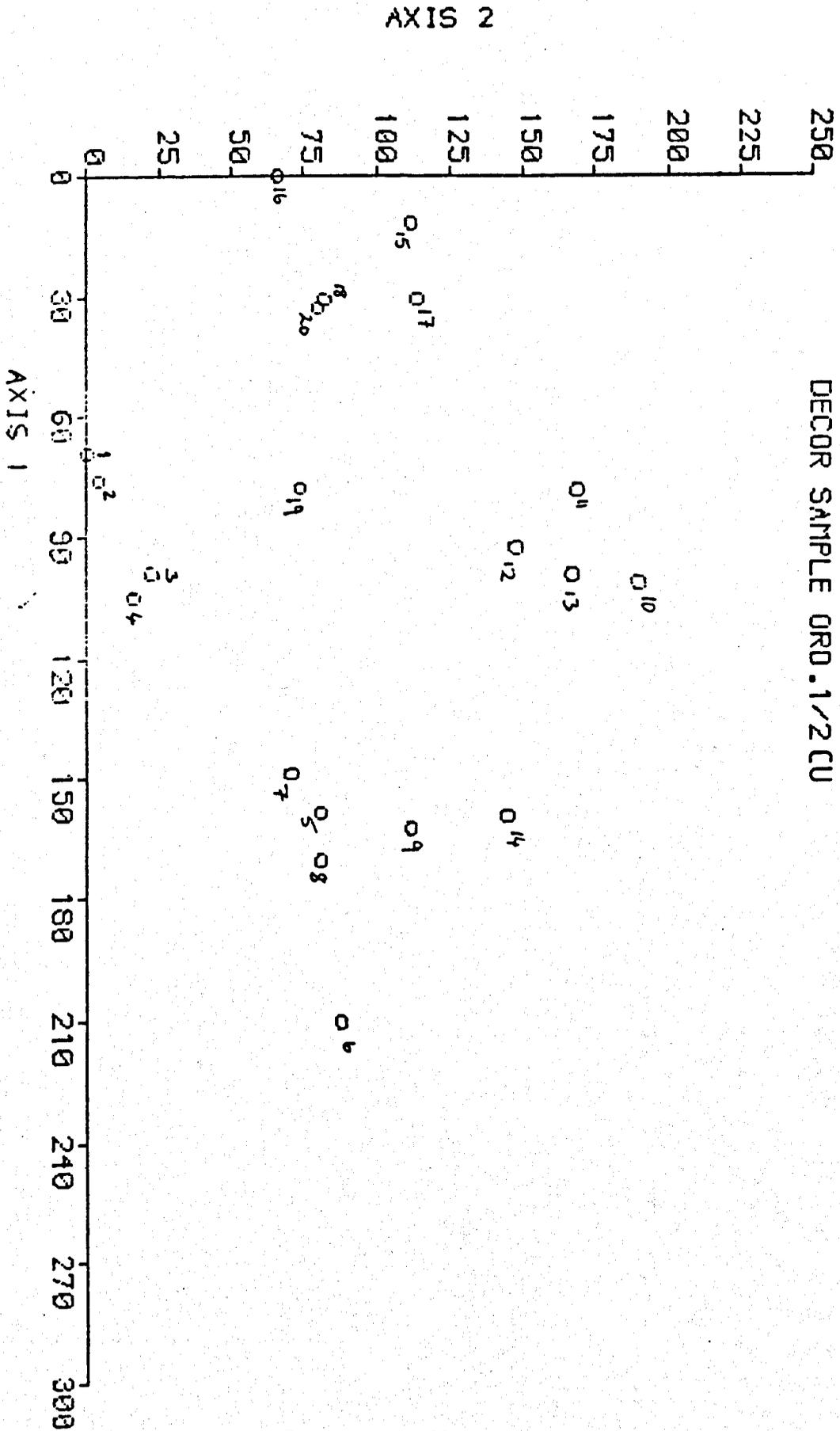


Figure 1.26 b Decorana ordination of Culross samples on first two axes.

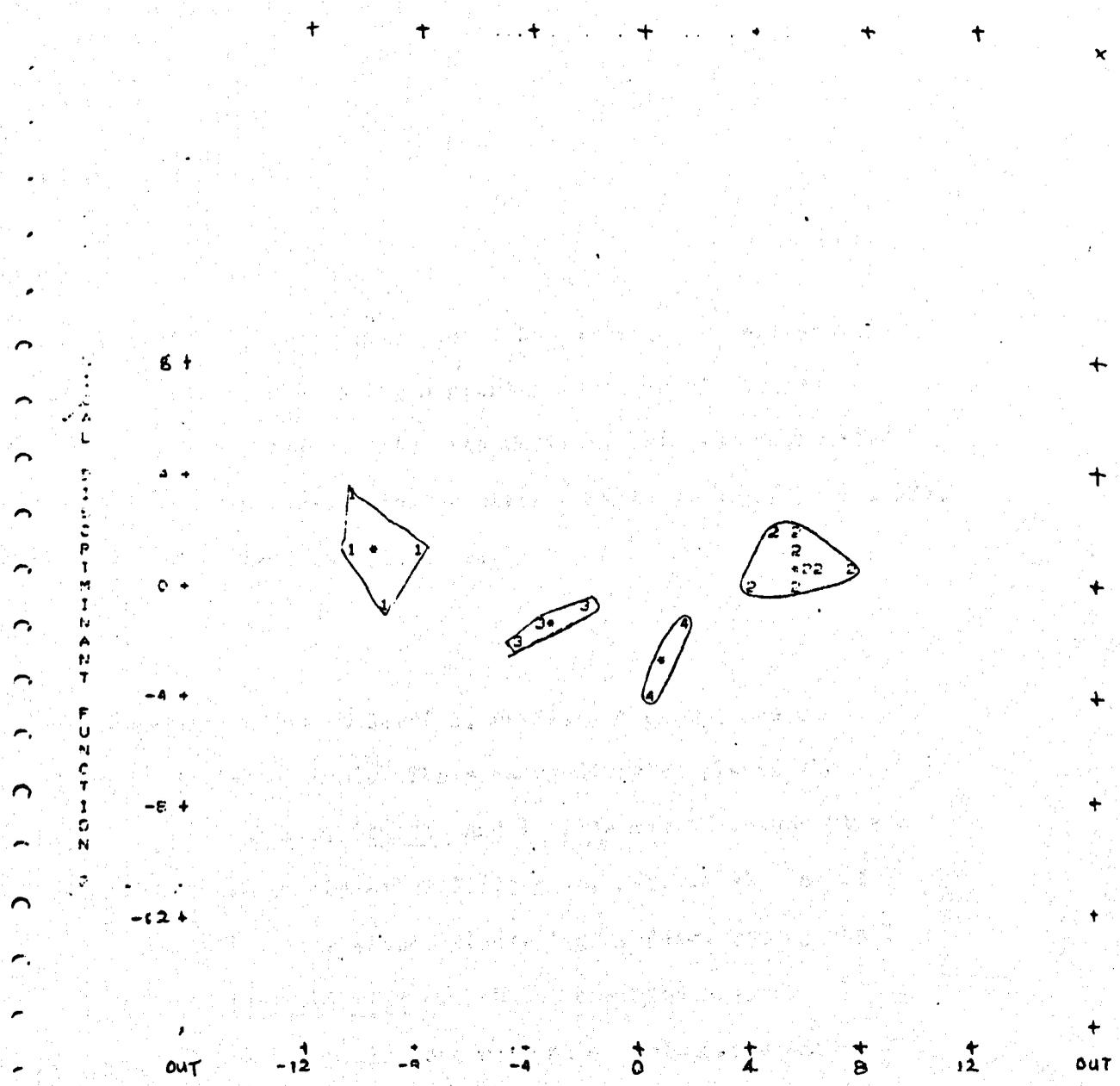


Figure 1.26 c MDA : CULROSS

separated in discriminant space (Fig.1.26c). Date appeared to account for most of the separation. Tide was not an influential variable at Culross. The first two discriminant functions accounted for 95.8% of the variance, and 100% of samples were correctly reclassified.

Skinflats

There were 20 samples in this group. DCA axis 1 was considerably longer than axis 2, indicating a greater turnover of species along this axis (Fig.1.27b). As with Culross, Date was correlated with both axes. Disch was highly correlated with axis 2 (Table 1.13), while Chla and Ar were correlated with axis 1.

TS division was carried to level 3, deriving 6 groups one of which was a singleton sample. The primary division placed the indicators Pseudocalanus, Sagitta and Acartia clausi on one side and Polydora larvae on the other (Table 1.16, Fig.1.27a). As at Culross, further division showed clustering by date, with group 1 characterised by Maranzelleria, which was confined almost exclusively to this group. In contrast, other polychaete larvae were confined mostly to group 5. Samples in groups 1, 2 and 3 contained, in general, mostly neritic/marine taxa. Oithona and Pseudocalanus were present in most samples at Skinflats.

Table 1;16 Twinspan classification of Skinflats samples

SK

		111	11112	1	11	
		678345	167890	24591	302	
10	ACAR TONS	---	223	-22-1	-----	000000
21	PARA PARV	---	1	-----	-----	000000
9	ACAR LONG	---	3	-3--1	-----	000001
24	OIKO DIOI	---	2	-121	-----	000001
42	NUDI JUVE	---	1	1-----	-----	000001
4	NEOM INTE	---	---	-----1	-----	00001
19	CALA HELG	1	---	---11	-----	00001
8	ACAR CLAU	32	-2-	-2-12	-----	0001
13	ACAR DISC	-1	---	-1-----	-----	0001
30	MARA TROC	3	---	-----	-----	0001
31	MARA EGGS	4	---	-----	-----	0001
16	PSEU ELON	312	112234423	2--12	---	001
23	SAGI ELEG	311	1-1-1211111	---	---	001
29	MARA WIRE	446	---	-----3	---	001
17	OITH SIMI	2-3	2233332-2	23-12	-1-	010
39	CIRR CYPR	---	122	-----1	-----2-2-	010
5	EURY AFFI	444	112343433	45444	132	011
20	TEMO LONG	322	1-2123211	32--3	--2	011
32	LITT CAPS	311	--2	--1-	--111	011
40	CIRR NAUP	313	2222211-1	22-13	-2-	011
12	ACAR INER	-33	---	2221111	12-24	10
27	HARP SPEC	244	-23332232	43344	445	10
33	LITT VELI	212	---	-----	---13	10
35	SYLL SPEC	--1	---	-----	---1	10
26	ROTI SPEC	-4-	2---	4442-	65444	42- 110
28	POLY CILI	---	213	---	12244	222 110
2	BOSM SPEC	---	---	-----	-1-	1110
18	CENT HAMA	---	---	-----	-2--3-	22 1110
37	TERE LARV	---	---	-----	---1-11	11110
22	CYCL SPEC	---	---	-----	---1-	11111
36	ETEO LARV	---	---	-----	---1	11111
38	NERE LARV	---	---	-----	---1-23	11111
41	BIVA LARV	---	---	-----	---1-222	11111
		000	000	000000	11111	111
		000	111	1111111	00000	111
		000	1111111	00001		
			000011			

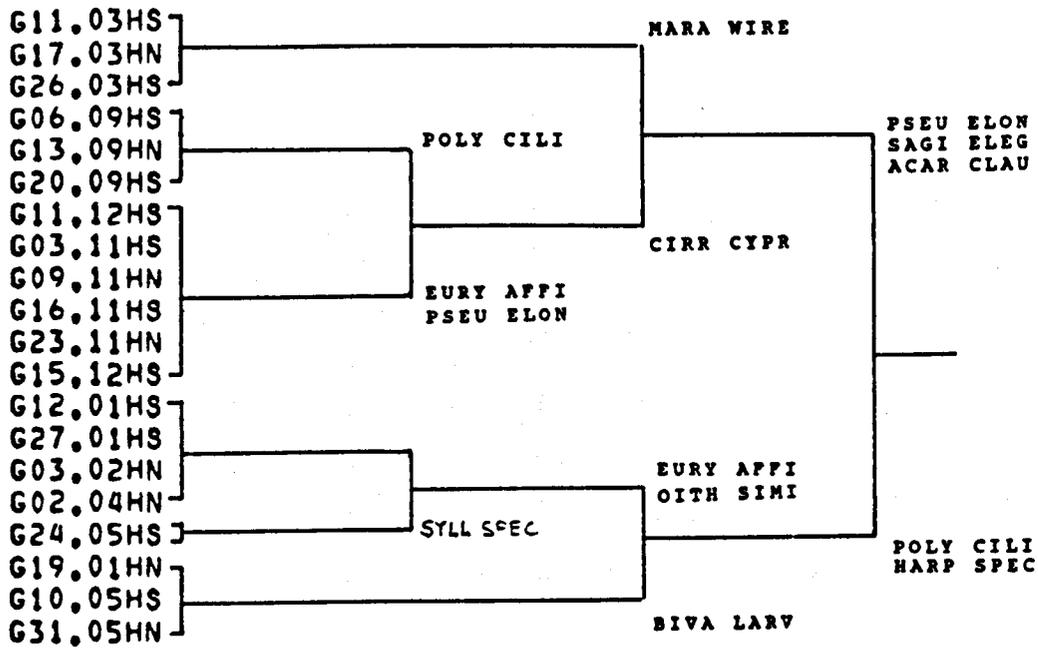


Figure 1.27 a

Dendrogram of Skinflats samples classified by Twinspan. Indicator species for each division shown.

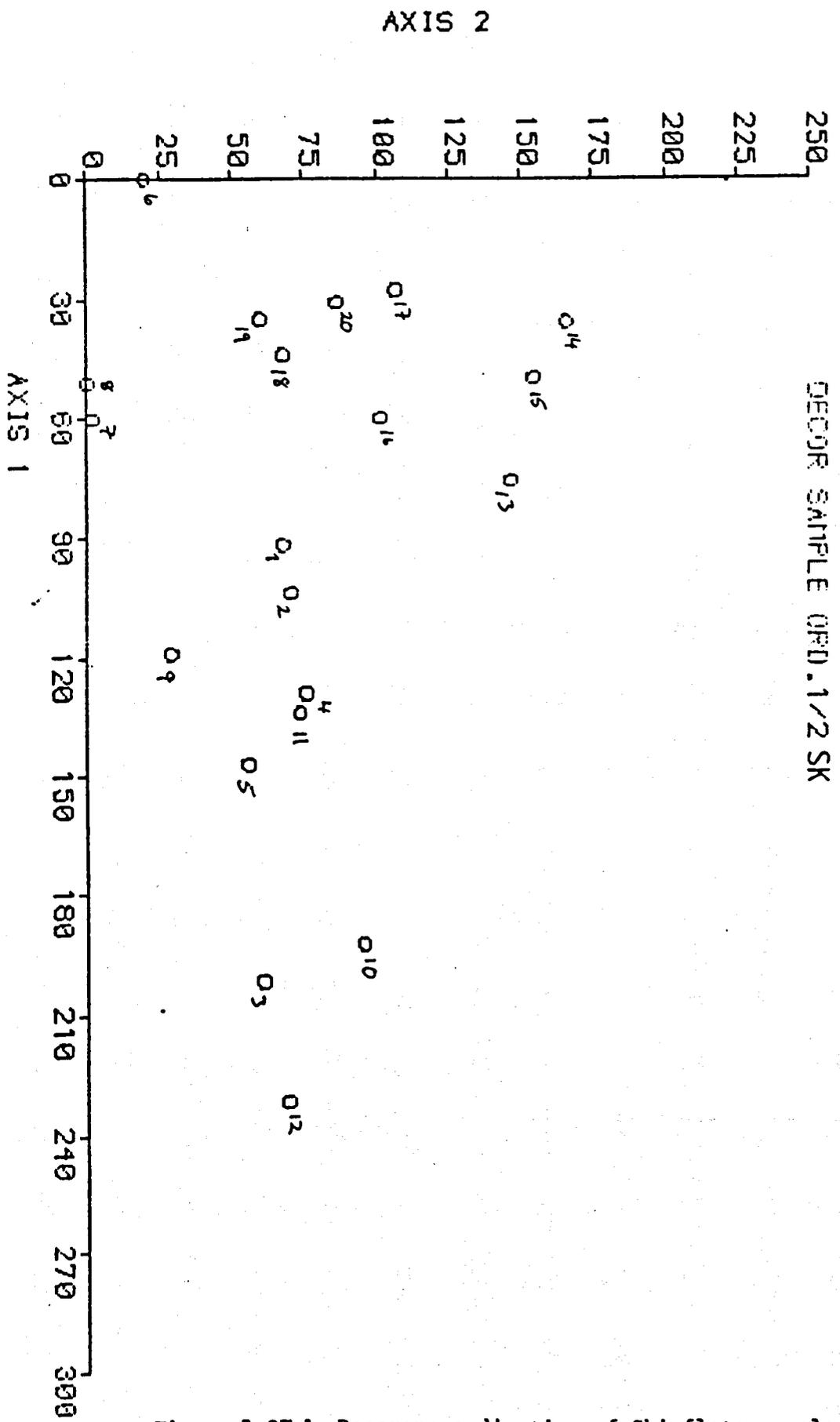


Figure 1.27 b Decorana ordination of Skinflats samples on first two axes.

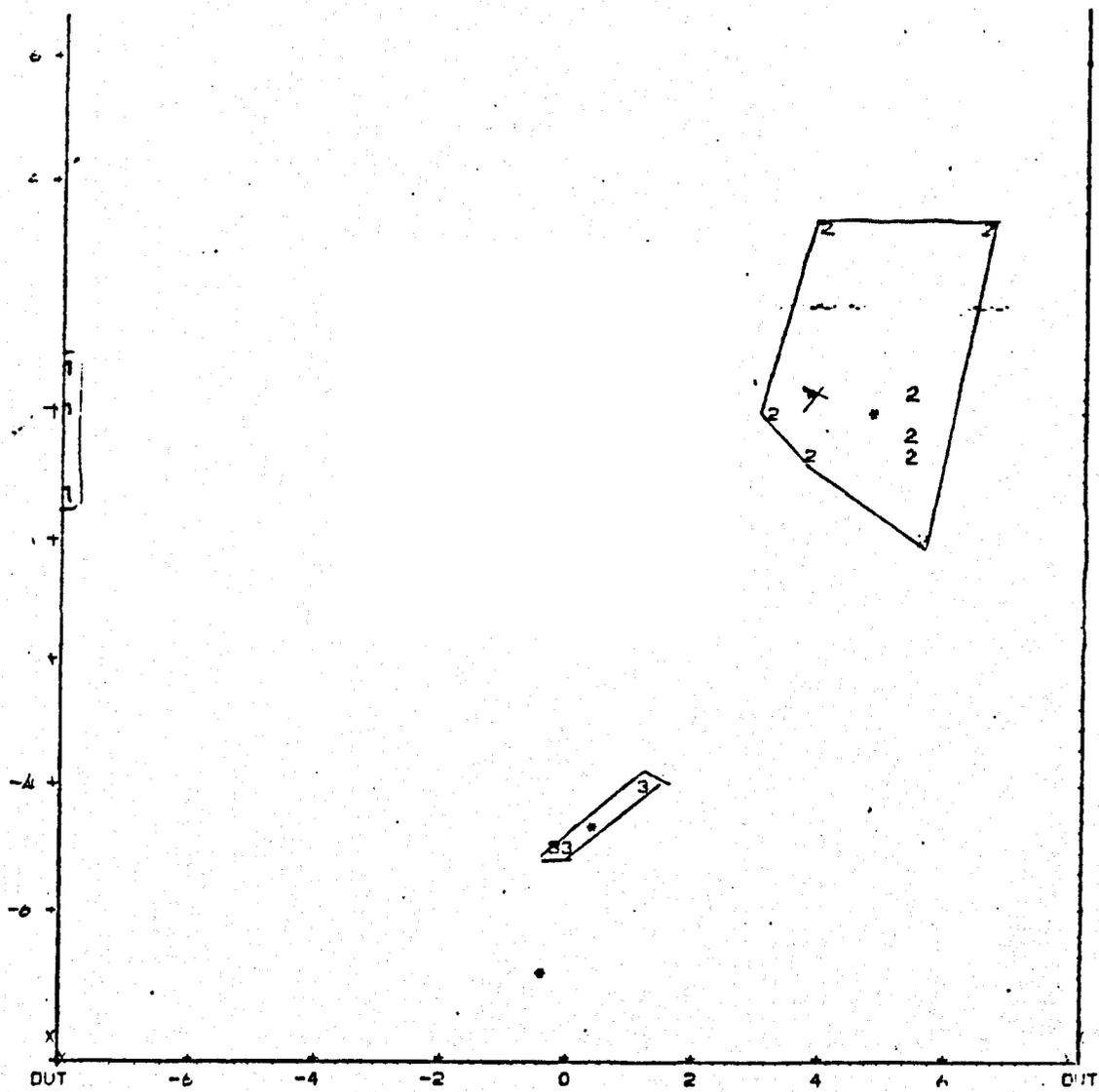


Figure 1.27 c MDA : SKINFLATS

MDA was carried out on TS groups defined at the second level of division (four groups). Date, Disch and Temp all had significant between-group F-ratios (Table 1.10). Date and Disch were positively related to Function 2, while on Function 1 all three appeared to have equal influence (Table 1.11a). Discrimination was again very effective with 93.7% of variance explained by the first two functions and 100% correctly reclassified, but in contrast to the DCA analysis, no influence of Chla or AR was observed.

Skinflats, like Culross, appears to be subject to seasonal rather than semilunar influences, despite the entrainment of abundance of eggs and larvae of some taxa already noted.

Kincardine

A total of 46 samples were taken at Kincardine.

Axis 1 represented a greater species turnover than axis 2 (Figure 1.28b). Date, Sal, Temp, Chla and AR were all significantly correlated with axis 1, while Disch was significantly correlated with axis 2 (Table 1.13).

TS classification was taken to three levels (eight groups). The main division was characterised by Maranzelleria, which was confined to groups 7 and 8 (March and April), while the other side of the division was dominated by the neritic copepods and meroplanktonic larvae excluding Maranzelleria (Table 1.17, Fig.1.28a).

Oithona and cirripede nauplii were present in the majority of samples, but cirripede cyprids were largely confined to group 1.

Eurytemora, Rotifera, and harpacticid copepods occurred in almost

Table 1.17 Twinspan classification of Kincardine samples

KI

	2223222	2223334	233334334	4 4 4	14	11111	1111	
	7041246	41350691	952382475	9068416	7132350	2456	3789	
4 NEOM INTE	-----	-----	12121	-----1	-----	-----	1	0000
16 PSEU ELON	--1--121	-----1313	-----11-22	-----	-----21	-----1	1	0000
10 ACAR TONS	-----	-----23-22112	-----	-----	-----	-----	-----	00010
11 ACAR BIFI	-----	-----1	-----	-----	-----	-----	-----	00010
19 CALA HELG	-----	-----1	-----1	-----	-----	-----	-----	00010
24 OIKO DIUI	-----	-----321	-----	-----	-----	-----	-----	00010
9 ACAR LONG	1-2--2	-----12-2	-----2111-11	-----	-----	-----	-----	00011
18 CENT HAMA	212-111	-----2-4	-----	-----	-----	-----	-----	00100
28 POLY CILI	33224352	-----234111	-----1--221	-----	-----	-----	-----	00100
36 ETEO LARV	2-1----	-----12-2	-----	-----	-----	-----	-----	001000
38 NERE LARV	22-----	-----332	-----	-----	-----	-----	-----	001000
41 BIVA LARV	3-21-11	1222-----	-----1-----	-----1-----	-----	-----	-----1	001010
13 ACAR DISC	--1-----	-----	-----	-----	-----	-----	-----	001011
21 PARA PARV	1-----1	-----	-----	-----	-----	-----	-----	001011
33 LITT VELI	2-1-2-2	-----1--1	-----	-----	-----	-----	-----	001011
35 SYLL SPEC	-----1	-----	-----	-----	-----	-----	-----	001011
42 NUDI JUVE	2-----	-----	-----	-----	-----	-----	-----	001011
34 APHR LARV	-1-----	-----1-1	-----1-----	-----1-----	-----	-----	-----	0011
37 TERE LARV	22--222	-----1	-----	-----1	-----12	-----	-----	0011
39 CIRR CYPR	3122222	-----2-3	-----11-----	-----1	-----1	-----4	-----	0011
12 ACAR INER	--2-33	-----1-2-2	-----	-----1	-----12	-----3	-----	01
17 OITH SIMI	2121--2	-----33332	-----1-22112	-----1--121	-----112	-----2-1211	-----	01
23 SAGI ELEG	-----1	-----1	-----	-----	-----	-----1	-----	01
40 CIRR NAUP	-333332	21114211	32-11-222	-----1122	1112222	2223-222	-----	01
5 EURY AFFI	4321443	3445-423	122333223	3323324	3333343	43343433	10	10
20 TEMO LONG	212-1222	-----1212	-----11	-----	-----2312222	2211	10	10
27 HARP SPEC	4322121	34332222	112212--12	3223232	221-242	22-22-3	10	10
32 LITT CAPS	-22--1	-----1	-----	-----	-----1	-----11-111	10	10
1 DAPH SPEC	-----	-----	-----1	-----2	-----	-----	110	110
2 BOSM SPEC	-----	-----	-----	-----1	-----111	-----	110	110
3 DIAP GRAC	-----	-----1	-----2	-----2	-----	-----11-1	110	110
26 ROTI SPEC	-----2	4245--1	-----322-12	4333423	5623555	42333-2	110	110
8 ACAR CLAU	-----2	-----111	-----	-----1	-----	2221	1110	1110
22 CYCL SPEC	-----	-----	-----	-----	-----	1--1	1111	1111
29 MARA WIRE	-----	-----1	-----	-----	-----1	-----22534	4433	1111
30 MARA TRCC	-----	-----	-----	-----	-----	-----142-4	3311	1111
31 MARA EGGS	-----	-----	-----	-----	-----	-----1-3	4311	1111
	0000000	0000000	0000000	0000000	1111111	1111111	1111	1111
	0000000	0000111	1111111	1111111	0000000	0000000	1111	1111
	0000000	1110000	1111111	1111111	0000000	1111111	0000	1111
	0111111		00000111	0111111	10001111			
	000111		001111	011111				
				00011				

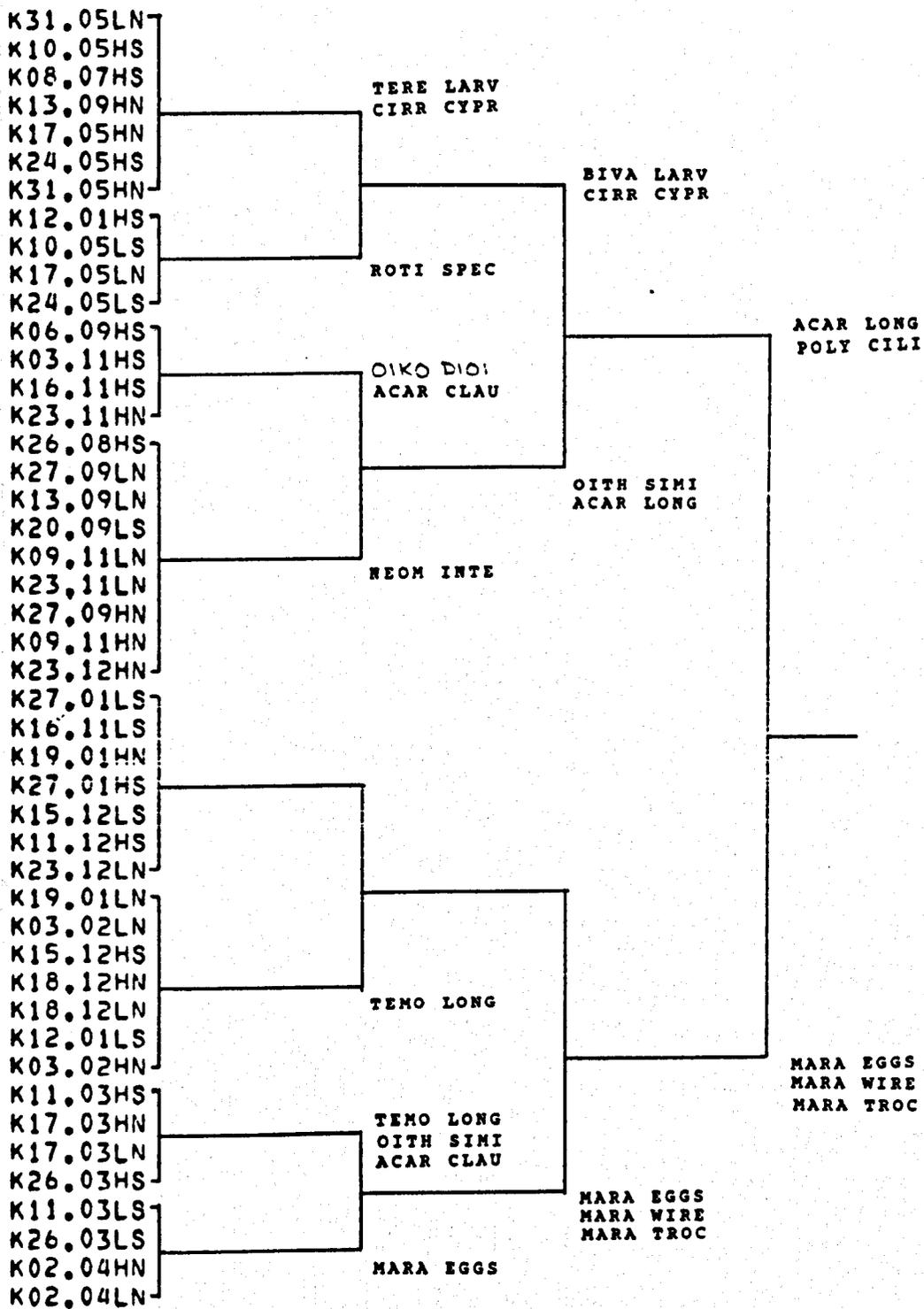


Figure 1.28 a

Dendrogram of Kincardine samples classified by Twinspan. Indicator species for each division shown.

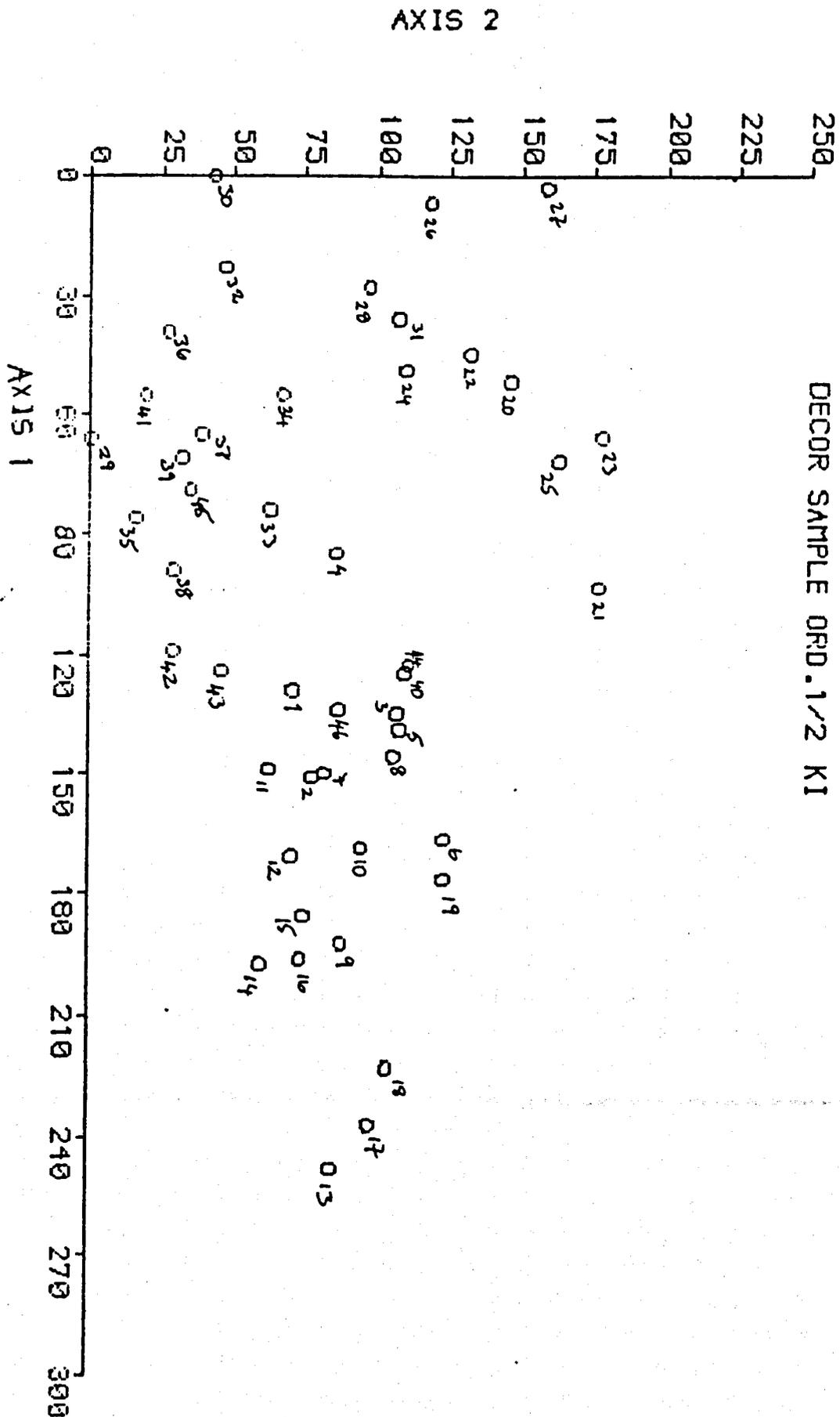
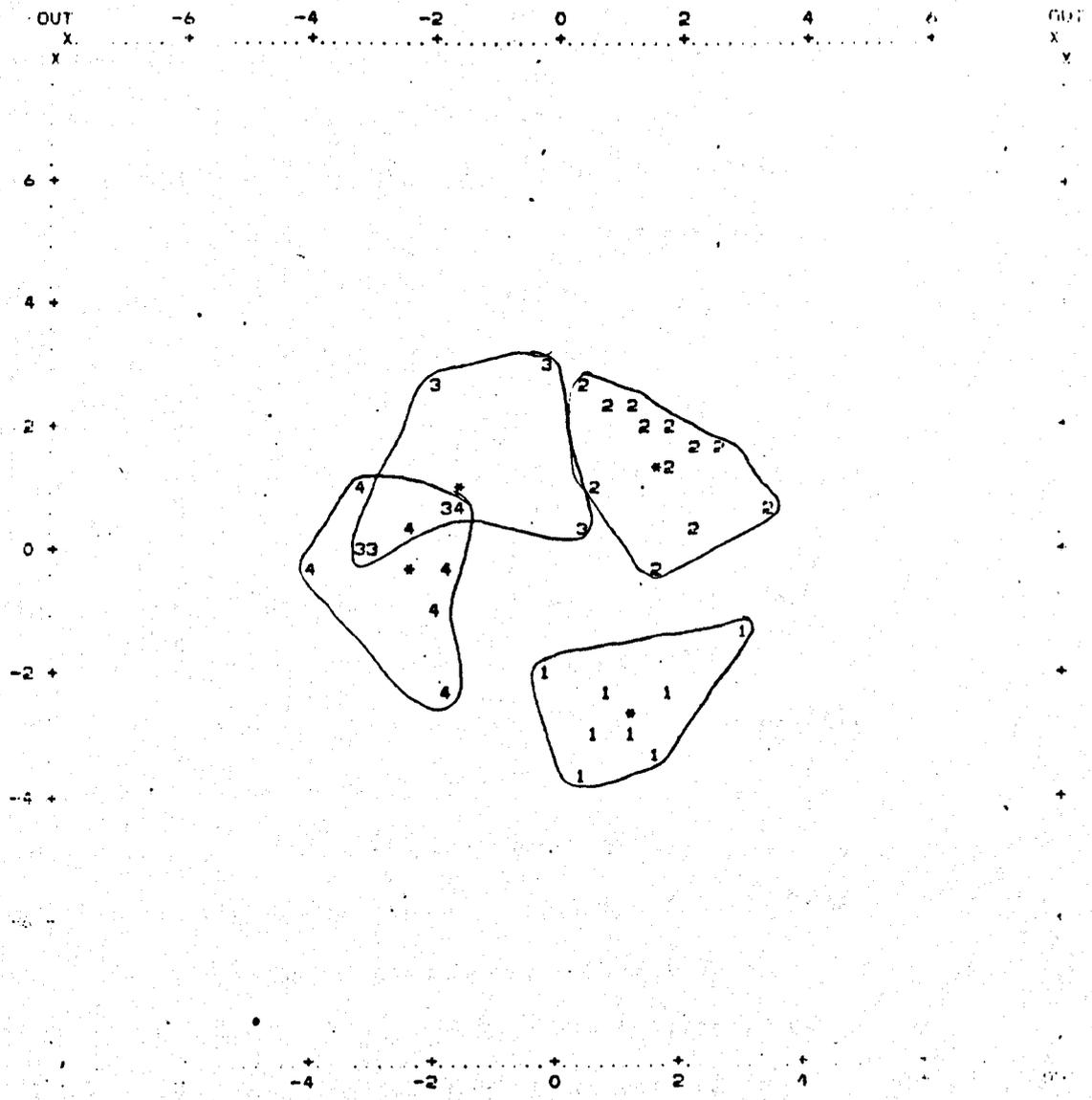


Figure 1.28 b Decorana ordination of Kincardine samples on first two axes.

CANONICAL DISCRIMINANT FUNCTION



DEC VAX-11/780 VMS V3.6

Figure 1.28 c MDA: KINCARDINE

all samples; Rotifera showed some bias toward the right-hand side of the major division (Table 1.18) and thus had restricted overlap with the neritic/lower estuarine community.

At level 3, there was some tendency for high tides to be sorted into group 1 and low tides into group 2. The same relationship applied to groups 3 and 4. Groups 1 and 2 were mainly May/June/September, while groups 3 and 4 were mainly September/November. Groups 5 and 6 contained predominantly samples from January and December and groups 7 and 8 from March and April.

MDA was carried on level 2 TS classification. Date, Disch, Chla AR, Sal and Temp all had significant between-groups F-ratios (Table 1.10). The groups were well-discriminated by MDA (Fig.1.28c), with 91.1% of the variance explained by the first two discriminant functions and 91.2% of samples successfully reclassified using the linear discriminant rule (Table 1.11b). Temp and AR were the most strongly related variables on function 1, and Disch and Sal on function 2. Thus, groups 3 and 4 (5,6,7,8 as described above) were associated with lower temperature and lower primary production than 1 and 2 (1,2,3,4 as described above) while groups 2 (3,4) and 3 (5,6) were associated with higher freshwater discharge and lower salinity than groups 1 (1,2) and 4 (7,8). TS/MDA predicts that the neritic/meroplanktonic assemblage should be associated with higher temperatures and higher primary production; this is the case on the left-hand side of the division (Fig.1.28a), and MDA further correctly summarises the

distinction between 1 (1,2) and 2 (3,4) in respect of higher discharge and lower salinity in the latter. The biological grouping shows a considerable reduction in diversity between these sample classes, with most of the larval forms not present, copepods such as Centropages and Temora reduced in frequency of occurrence and species such as Pseudocalanus and Acartia becoming more common.

Dunmore

There were 48 samples in the Dunmore data set.

Axis 1 of the DCA ordination (Fig.1.29b). was some 35% longer than axis 2. There was no obvious clustering of samples, but sample 29 (D26.08HS) was an obvious outlier; only 3 taxa occurred in this sample. Sal, Temp, Chla, AR, Tide, and Date were all correlated with axis 1, and Sal was also significantly correlated with axis 2 (Table 113.)3.

The major (level 1) division in TS was uneven (Table 1.18, Fig. 1.29a), and was defined mainly by the fidelity of A.clausii, A.longiremis, Polydora larvae, cirripede cyprids , Centropages, terebellid larvae and A. bifilosa inermis to the right side versus a loose association of freshwater species, Neomysis and Maranzelleria on the left.

Groups 1 and 2 were predominantly low tide samples. and mainly

collected in November/December/January. These groups were characterised by high Rotifera abundance and distinguished by the association of Diaptomus and Bosmina in group 1. Groups 3 and 4 differed from 1 and 2 by virtue of increased presence of cirripede nauplii; group 3 was a cluster of samples containing Maranzelleria larvae and Littorina egg capsules, while group 4 contained an association of Pseudocalanus, Oithona and Temora. Groups 3 and 4 were mostly high tide samples, and from the March and December collections. Groups 5 and 6 displayed the highest diversity, with a high frequency of occurrence of A.longiremis, Polydora larvae, Cirripede cyprids, Centropages, terebellid larvae, nereid larvae and A.bifilosa inermis. These two groups differed little, and primarily in respect of the occurrence of terebellid larvae. Groups 5 and 6 were, like 7 and 8, predominantly high tide samples collected in May-September.

MDA was carried out on level 2 TS classification; MDA group 1 is therefore equivalent to TS groups 1 and 2, and so on. Tide, Date, Chla, AR, Disch, Sal and Temp all had a significant between-groups F-ratio; from Culross to Dunmore the number of significant variables increased from 4 to 7. Temp, AR, Chla were positively associated with discriminant function 1, and Disch was negatively associated with this function. Sal, Tide, and Date were negatively associated with function 2 (Table 1.11a). The first two discriminant functions accounted for 84.1% of the total variance, and samples were reclassified with 81.1% success (Table 1.111.11b).

Fig. 1.18 Twinspan classification of Dunmore samples

DU

	114	12244	2333444	1	21111	4444	11223	222	2333	333		
	79139	9353567679147358024			12467	0268158588024	9135	024				
5 EURY AFFI	34443	6565245232444343344			34445	4434445	434455	-233	-22		00	
27 HARP SPEC	22233	445432-12-222342233			42133	1322322	332222	-231	12-		00	
32 LITT CAPS	---1-	1-----12--1-			121-1	-----12-	1-----				00	
36 ETEO LARV	-----	2-----			1-----	-----	-----1				00	
29 MARA WIRE	-1-2-4	-----1--1			24443	-----35	-----3				010	00
30 MARA TROC	-----	-----			3-33	-----	-----				010	00
31 MARA EGGS	---2-	-----			4-43	-----	-----				010	00
33 LITT VELI	-----	-----			11-2-	-----1	-----1				010	00
1 DAPH SPEC	12-1	-----			1-----	-----1	-----				010	01
3 DIAP GRAC	23222	---1-----			1-----	-----	-----				010	01
15 CHYD SPEC	-----	1-----			-----	-----	-----				010	1
22 CYCL SPEC	2-----	1-1-----1-			-----	-----	-----				010	1
26 ROTI SPEC	355224	-54444-1-425455555			-3-53	33443-32	-2223	---	2---		010	1
2 BOSM SPEC	12211	-----			-----	-----	-----111	---			011	
4 NEOM INTE	-----	1122-1-11221			-----	-----	-----11	---	3-2-12		011	
8 ACAR CLAU	-----	-----			-----	-----	-----		2-		100	00
10 ACAR TONS	-----	-----			-----	-----	-----		2222323		100	00
24 OIKO DIOI	-----	-----			-----	-----	-----		1-2		100	00
9 ACAR LONG	-----	-----1-----			1-----	1-----	1123-1	---	22		100	01
23 SAGI ELEG	-----	-----			-----	-----	1-2	---	1		100	01
28 POLY CILI	-----	12-----			-----	-----	31-323	---	21-2		100	01
39 CIRR CYPR	-----	1-----			12-----	-----	2-323	---	1-2		100	01
18 CENT HAMA	-----	-----			-----	-----	21-323	---	11		100	100
19 CALA HELG	-----	-----			-----	-----	1-1	---			100	101
21 PARA PARV	-----	-----			-----	-----	2-	---			100	101
34 APHR LARV	-----	-----			-----	-----	1-	---			100	101
37 TERE LARV	-----	-----			-----	-----	112	---			100	101
38 NERE LARV	-----	1-----			2-----	-----	21-222	---			100	101
42 NUDI JUVE	-----	-----			-----	-----	1-	---			100	101
12 ACAR INER	-1-----	-----			-----	11-1111	122	---			100	11
41 BIVA LARV	-----	1-----			-----	-----	1-	---			100	11
40 CIRK NAUP	-----	11-----1-----			112-1111213	211213	1212212				101	
16 PSEU ELON	-----	-----			2-11	2221331	1223-3	---	11-		11	
17 OITH SIMI	-----	11-----1-----			22-2	22223-123	22-3	---	112		11	
20 TEMO LONG	-----	1-----			2-1-1	11-12-1111	3-3	---	1		11	
	00000	000000000000000000000			000000	0000000	1111111	1111111	1111111			
	00000	000000000000000000000			111111	1111111	0000000	1111111	1111111			
	00000	111111111111111111111			000000	1111111	0001111	0000111				
	00011000	111111111111111111111			0111110000011							
		0000000000111111			00001							
		00111111111000011										

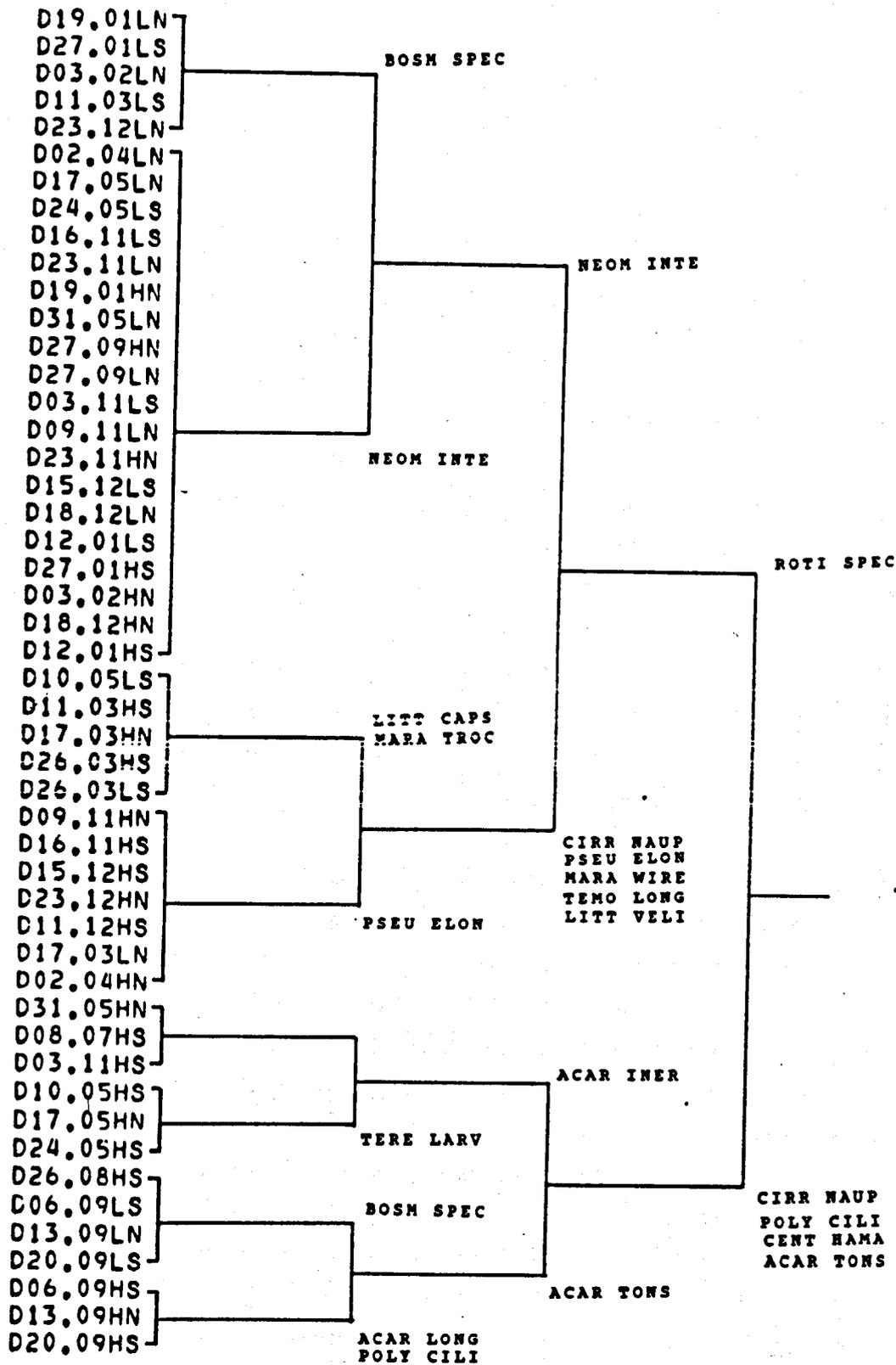


Figure 1.29 a

Dendrogram of Dunmore samples classified by Twinspan. Indicator species for each division shown.

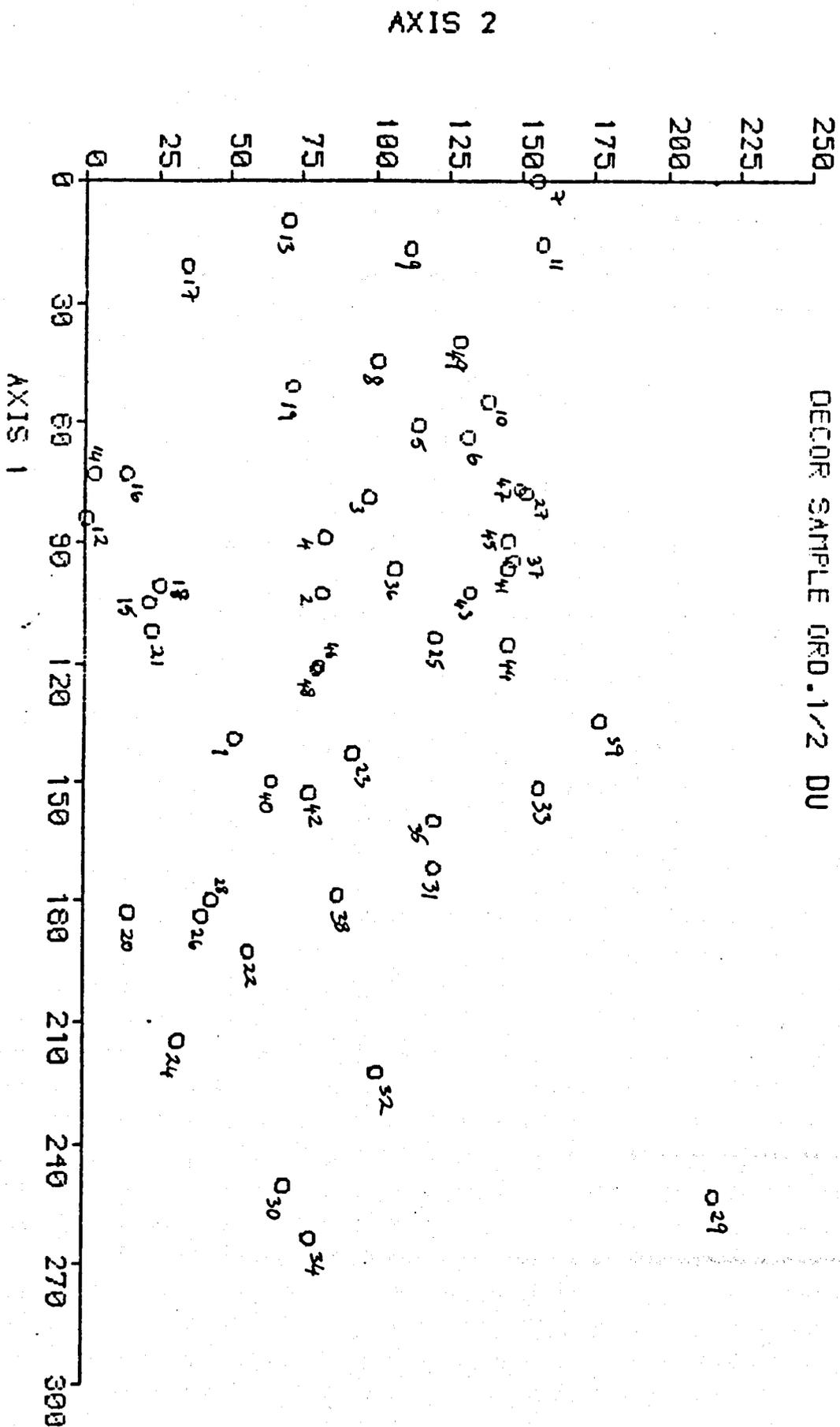
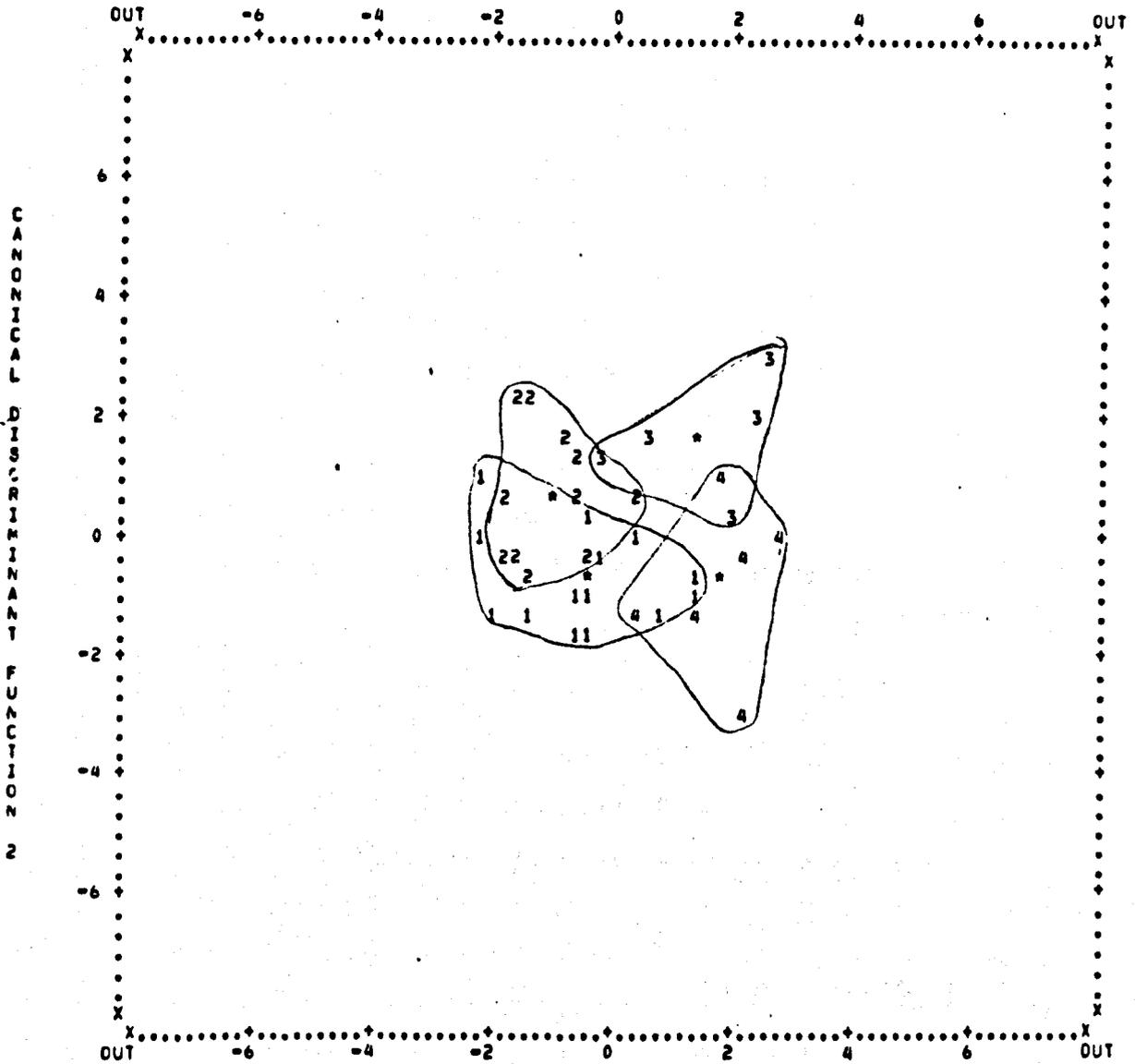


Figure 1.29 b
Decorana ordination of Dunmore samples on first two axes.

ALL-GROUPS SCATTERPLOT - * INDICATES A GROUP CENTROID

CANONICAL DISCRIMINANT FUNCTION 1



4-DEC-84 MDA DU TS

Figure 1.29 c MDA: Dunmore

The groups ordinated by MDA were less clearly defined than in the stations considered previously, and analysis at TS level 3, with eight groups might have been more successful. Nevertheless, considering the structure matrix summary (Table 1.11b), MDA predicts that group 3 (TS 5,6) should have earlier date and higher salinity than group 4 (TS 7,8), and this is in fact correct.

Dunmore showed an increased degree of tidally- and primary production-associated structure in comparison with stations further down the estuary.

South Alloa

A total of 49 samples were taken at S.Alloa.

The DCA axes were approximately equal in length, indicating the same amount of species turnover along each axis (Fig.1.30b). Tide, Sal, Temp, Chla, Date and AR were strongly correlated with axis 1 and Sal also showed a degree of association with axis 2; this pattern was similar to that at Dunmore (Table 1.13)3.

The major TS division was indicated by Neomysis and Diaptomus versus Eurytemora, cirripede nauplii, Polydora, Oithona and Maranzelleria, but sample diversity was generally low (Table 1.19). Group 1 was defined at level 2, and was characterised by the presence of Acartia tonsa, whilst group 2 was characterised by cyclopid copepods. Group 3 contained the majority of occurrences of Diaptomus, Daphnia and Bosmina. Group 4 had few freshwater

taxa, but contained some Oithona, Polydora larvae and cirripede nauplii. Group 5 was distinguished by the joint occurrence of Oithona, Polydora, A.longiremis, Pseudocalanus, Temora, Centropages, and terebellid larvae, while groups 6 and 7 were similar to each other and differed primarily in respect of higher Eurytemora abundance in the former and the presence of Littorina egg capsules in the latter. Groups 6 and 7 contained the majority of Maranzelleria occurrences. Group 1 contained late summer/autumn samples and mainly high tide (Fig.1.30a). Groups 2 and 3 were predominantly winter samples with no significant bias to either high or low tides. Groups 4 and 5 were mainly May high tide samples, and were associated with the highest Eurytemora abundances as well as the majority of neritic copepods and meroplanktonic larvae. Groups 6 and 7 were exclusively March and April samples and mainly high tide; the only samples from March and April not included in this group were low tide.

MDA was carried out at TS level two, and the previous comments regarding group numbering apply. Date, Disch, %org, Ar, Sal, and Temp had significant F-ratios (Table 1.10). Sal was positively and Disch and %org negatively associated with function 1; Date, Chla and AR were negatively associated with function 2 (Table 1.11a).

The first two functions accounted for 93.9% of variance, and 85.5% of samples were correctly reclassified using the linear discriminant rule derived by the analysis. The sample groups were clearly distinguished in

Table 1.19 Twispán classification of South Aloa samples

SA

	233344	33342	1344344	14	13411	22 22	234222	11111	
	903405	1579	339867913	568902756413	15427	282804647826			
2 BOSM SPEC	----	1-1	-----1	---222---	1-22	-----	-----	-----	000
4 NEOM INTE	--31-	2-1112	-----2122	-2---	21	-----	1	-----	000
6 ACAR CLAU	---1	-----	-----	-----	-----	-----	-----	-----	000
15 CHYD SPEC	-----	22	---1-1	-----	-----	-----	-----	-----	000
1 DAPH SPEC	-----	-----	-----	-1---	2111-1	-----	-----	2	001
3 DIAP GRAC	-----	3-2	-1-----11	12221-	221222	-----	11	2-1-	001
10 ACAR TONS	2312	-----	-----	-----	-----	-----	2	-----	001
22 CYCL SPEC	-----	2-1211	-----	-----	-----	11	-----	-----	001
5 EURY AFFI	232433	2322	534444223	4444354233432	55555	4534655	45544	01	
26 ROTI SPEC	-22332	2222	-33243222	5555465332442	-454-	64242542	-242	01	
27 HARP SPEC	2--2-	1221-	313133232	332222221	-22	333123212	22222232	01	
16 PSEU ELON	-----	11	-----	-----	-----	-----	11211	-----	100
39 CIRR CYPR	---1	--2-	1-----	-----	-----	-----	1-1-	112	100
17 OITH SIMI	-----	-----	-----	2-1	-----	-----	211111	1-11-	1010
28 POLY CILI	12	-----	-----	-----	1	12-2-	11-232	-----	1010
9 ACAR LONG	-----	-----	-----	-----	-----	-----	2--21	-----	101100
36 ETEO LARV	-----	-----	-----	-----	-----	1	-----	1	101100
38 NERE LARV	-----	-----	-----	-----	-----	12	-----	21	101100
42 NUDI JUVE	-----	-----	-----	-----	-----	2	-----	-----	101100
18 CENT HAMA	-----	-----	-----	-----	-----	-----	231	-----	101101
19 CALA HELG	-----	-----	-----	-----	-----	-----	1	-----	101101
37 TERE LARV	-----	-----	-----	-----	-----	-----	111	-1-	101101
20 TEMO LONG	-----	-----	-----	-----	1	1	12-2	-----	10111
40 CIRR NAUP	-----	-----	-----	-----	11	-1111	-2111	1-121	10111
30 MARA TROC	-----	-----	-----	-----	-----	-----	-----	33	1100
31 MARA EGGS	-----	-----	-----	-----	1	-----	-----	1-33	1100
33 LITT VELI	-----	-----	-----	-----	-----	-----	11	-2-1	1100
12 ACAR INER	-----	-----	-----	1	-----	-----	1	1-1-	1101
29 MARA WIRE	-----	-----	2-2	-----	2	11	-----	32544	1101
32 LITT CAPS	-----	1	-----	-----	21	-----	1	-----	111
	000000	0000	000000000	0000000000000	11111	1111	1111	1111	1111
	0000	111111	1111111111	1111111111111	00000	0000	0000	0000	11111
	000000	11111111	1111111111	1111111111111	00000	0000	111	00011	
	001111	000000000	1111111111111	00000	1111				
			0111111111	00000001111111	0111				
			000001110001	1111000011					

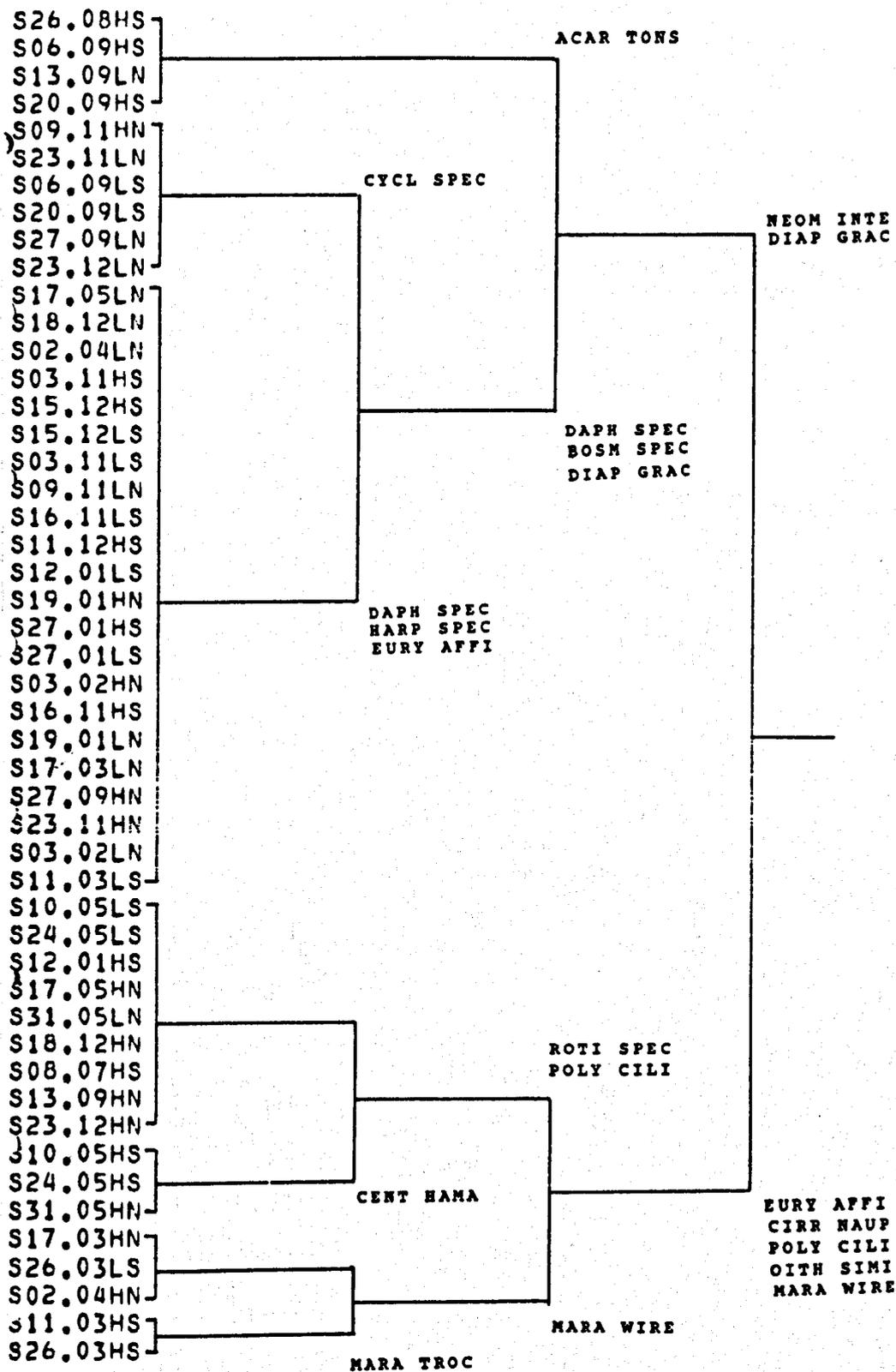
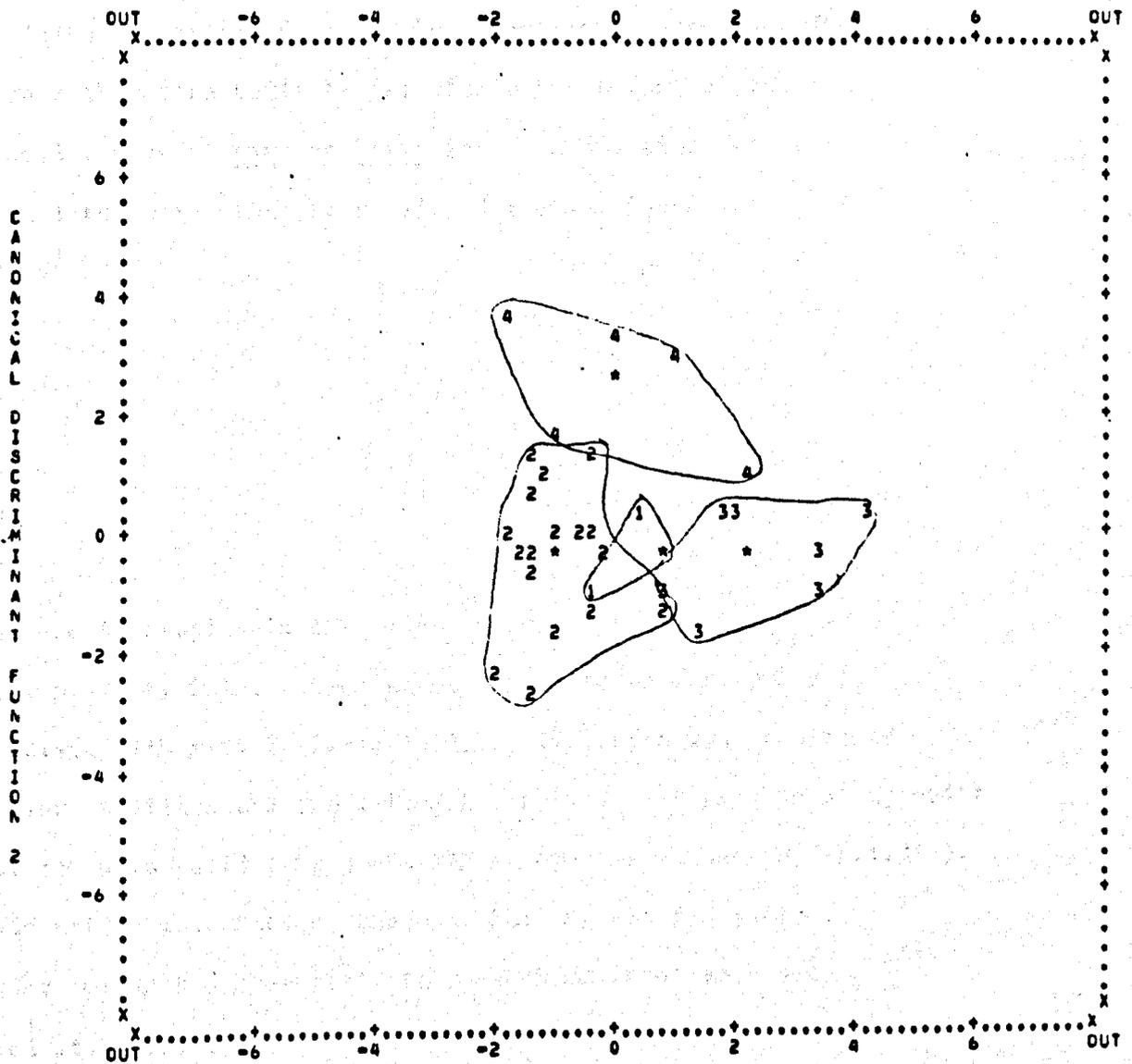


Figure 1.30 a

Dendrogram of S.Alloa samples classified by Twinspan. Indicator species for each division shown.

ALL-GROUPS SCATTERPLOT - * INDICATES A GROUP CENTROID

CANONICAL DISCRIMINANT FUNCTION 1



4-DEC-84 MDA SA TS

Figure 1.30 c MDA: S. Alloa

discriminant space, with 2 (TS 2 and 3) and 3 (TS 4 and 5) separated in terms of salinity and discharge (cf Fig.1.30c), and both of these distinguished from group 4 (TS 6 and 7) by virtue of the latter's earlier date and lower primary production. MDA function 2 therefore reflects faithfully the effect of the early-spring peak of Maranzelleria larval production, while function 1 reflects other seasonal and spatial factors.

Fallin

There were 42 samples in the Fallin group.

Date, Temp, Inor, Chla, Phaeo, AR were correlated with DCA axis 1, and Disch with axis 2 (Table 1.13). Axis length was comparable to previous stations and their lengths implied that samples at opposite ends of the axes would have about 25% of species in common (Fig.1.31b).

Sal was not an important variable at Fallin, but inorganic suspended solids and phaeopigments assumed an importance not observed at stations further down the estuary.

TS classification was carried to level three (Table 1.20). At level one, the main division indicates high abundance of Eurytemora on one side and the predominance of freshwater species on the other. Occurrences of Maranzelleria are almost evenly divided between groups 1 and 8 at level three. Group 2 was distinguished by the presence of Daphnia, Bosmina and Diaptomus in the relative absence of all other taxa except the common Eurytemora, harpacticids, and Rotifera. Groups 3 and 4 are mainly

distinguished by the clustering of most occurrences of Neomysis and chydorids, while groups 5 and 6 are characterised by high abundances of Rotifera and Eurytemora respectively. Group 7 consisted of 4 samples containing Littorina egg capsules, and as noted above group 8 was defined by occurrence of Maranzelleria. High and low tides did not appear to be segregated in any particular manner (Fig.1.31a).

Disch, Org, %org, Chla, Phaeo, Temp all had significant F-ratios (Table 1.10). Temp, Phaeo were positively associated with the first discriminant function (Table 1.11a), Disch and % org positively with function 2, and Date negatively with function 2. 89.9% of variance was accounted for by the first two functions (Table 1.11b) and 90.3% were correctly reclassified. MDA was carried out on level two TS groups; when plotted in discriminant space, groups 1 (TS 1,2) and 4 (TS 7,8) were clearly separated from each other and from the less well-separated groups 2 (3,4) and 3 (5,6).

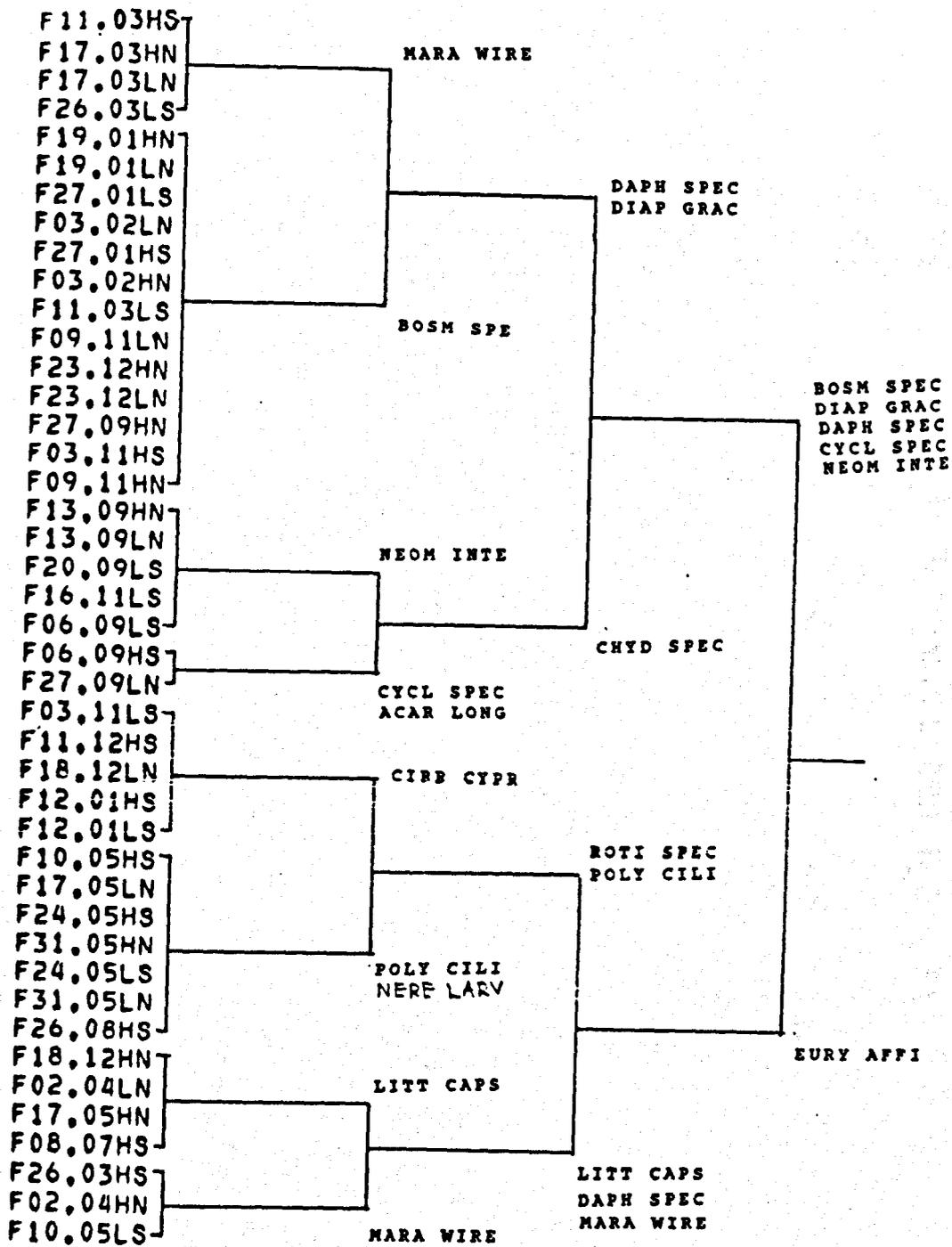


Figure 1.31 a

Dendrogram of Fallin samples classified by Twinspan. Indicator species for each division shown.

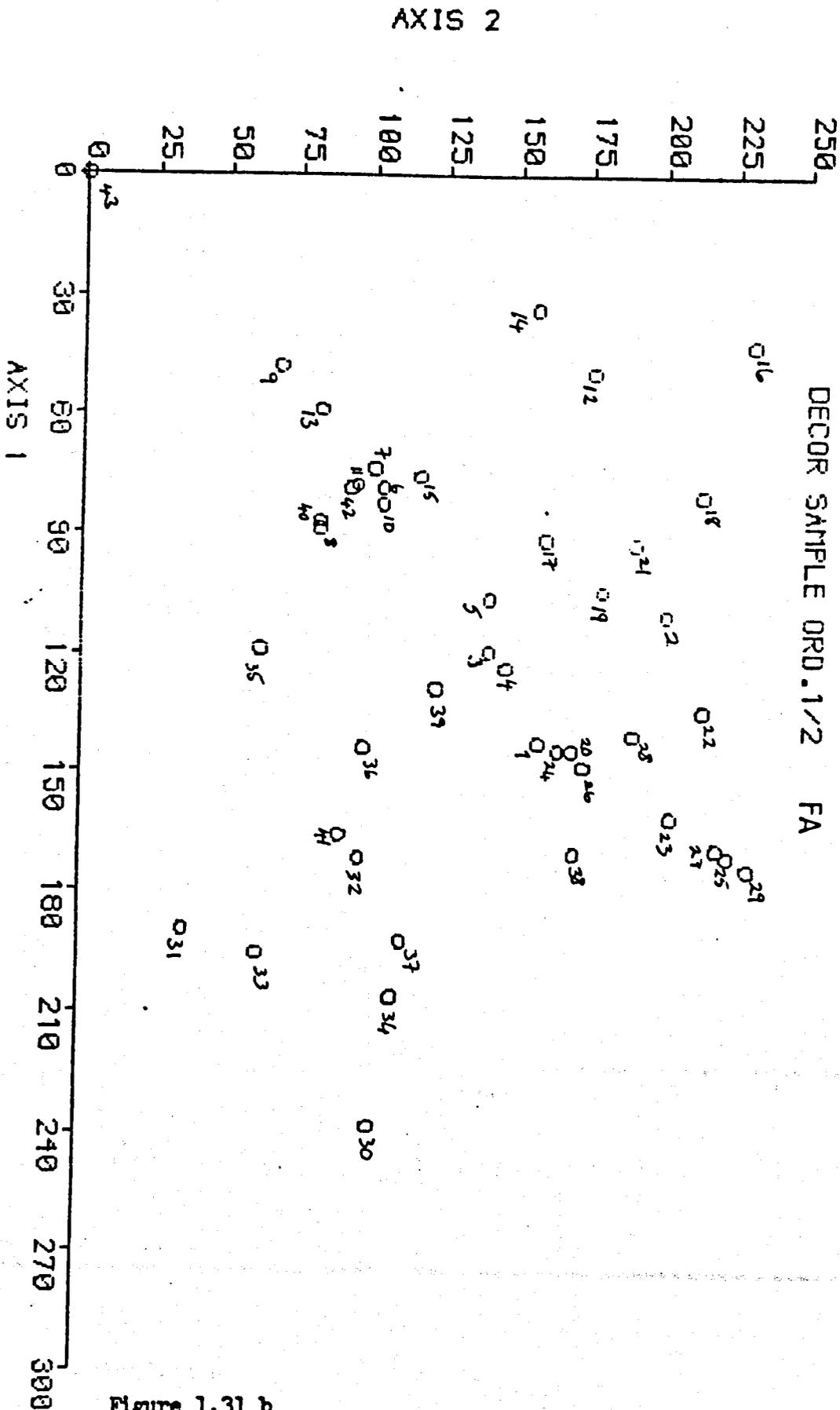


Figure 1.31 b

Decorana ordination of Fallin samples on first two axes.

Sampling cycle (spring-neap-spring-neap sequences)

Date groups 1,5,6 and 9 contained too few samples to analyse successfully. These correspond to December 1981, July 1982, August 1982, and December 1982. Analysis was completed for groups consisting of samples from January/February 1982, March/April 1982, May 1982, September 1982 and November 1982. The summer period was not therefore represented in this category.

Date group 2 (Jan-Feb 1982)

This group contained 36 samples

DCA axis 1 was dominant (Fig.1.32b), with some evidence of sample clustering. Dist, Sal, Temp, Inor Org, Phaeo were significantly correlated with axis 1 (Table 1.14) and Phaeo was also correlated with axis 2.

The main division at level 1 in TS was defined by the indicators Diaptomus on one side and cirripede nauplii on the other.

Diaptomus was associated closely with Bosmina (Table 1.21) and, to a lesser extent, with Daphnia, while the cirripede nauplii co-occurred to a large extent with the neritic copepods Oithona

Table 1.21 Twinspan classification of Date Group 2 samples

GP 2

	1	13	2	22	1123	1233	23332	1112221	
	129	35369	47080	1210859	32146	25656	483477		
41 BIVA LARV	-1	-----	-----	2	-----	-----	-----	-----	1111
28 POLY CILI	122	-----	-----	22	-----	-----	-----	-----	1111
40 CIRR NAUP	222	-11221	-1	-----	-----	-----	-----	-----	111011
23 SAGI ELEG	1-1	-----	-----	-----	-----	-----	-----	-----	111010
18 CENT HAMA	--2	-----	-----	-----	-----	-----	-----	-----	111010
17 OITH SIMI	223	2112	-----	-----	1	-----	-----	-----	111010
16 PSEU ELON	21	--2	-----	-----	-----	-----	-----	-----	111010
37 TERE LARV	-----	2	-----	-----	-----	-----	-----	-----	11100
30 MARA TROC	-----	1	-----	-----	-----	-----	-----	-----	11100
20 TEMO LONG	322	22322	-----	-----	-----	-----	-----	-----	11100
29 MARA WIRE	---	1-122	-----	1	-----	1	-----	-----	110
12 ACAR INER	1-2	---12	-1	-----	1	1	-----	-----	110
32 LITT CAPS	---	---1-2-1	-----	-----	2	-----	-----	-----	10
27 HARP SPEC	433	32242	34234	2222343	222221222	2222222	2222222	01	01
26 ROTI SPEC	645	55655	55344	3455563	556545435	3324433	01	01	
5 EURY AFFI	435	43343	54341	2433443	445433324	33233-2	01	01	
39 CIRR CYPR	-----	-----	-----	1	-----	-----	-----	001	
4 NEOM INTE	-----	-----	-----	-----	2	-----	2	001	
3 DIAP GRAC	-----	-----	-----	112	221222233	2222232	001		
2 BOSM SPEC	--1	-11	-----	-----	2222222	122313-	001		
22 CYCL SPEC	-----	-----	1	-----	-----	2-1	000		
1 DAPH SPEC	-----	-----	-----	1	1	2122222	000		
	000	000000	00000	11111111	111111111	11111111	11111111		
	000	000000	11111	10000000	00000	11111111	11111111		
	000	111111	00000	10000000	11111	000000	11111111		
	00011		0000011		00001	10000001			
			00001			000001			
						01111			

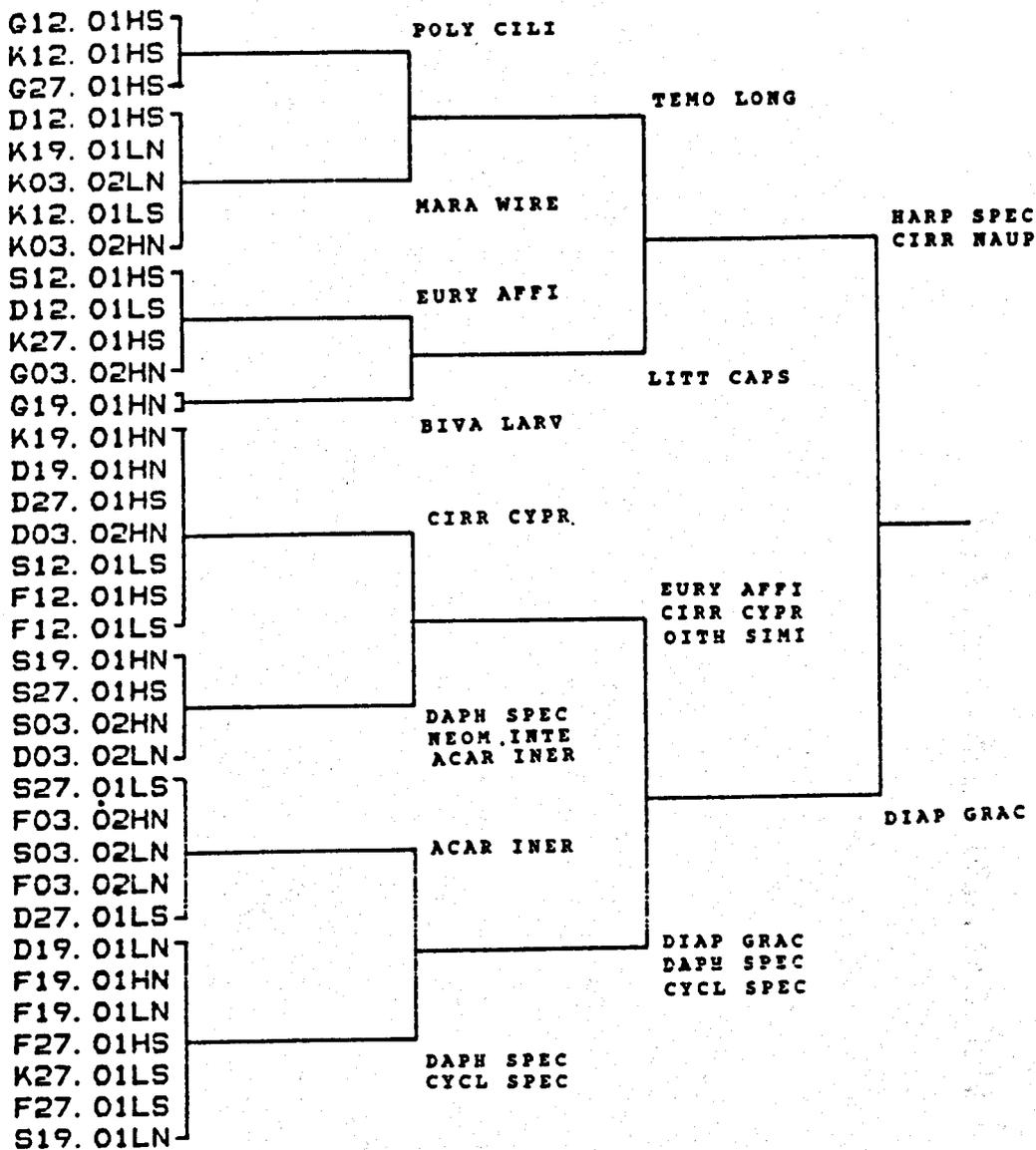


Figure 1.32 a

Dendrogram of Group2 samples classified by Twinspan. Indicator species for each division shown.

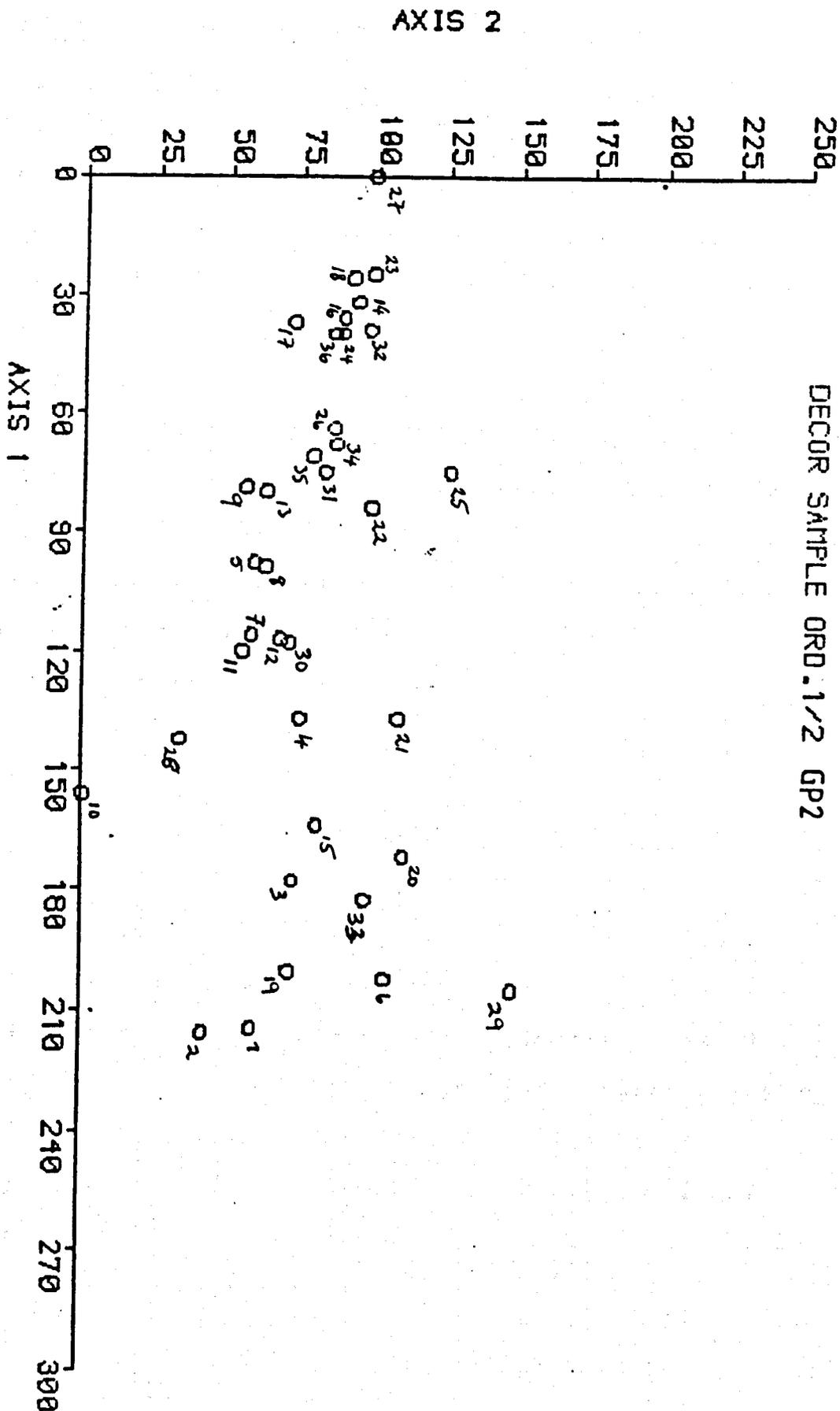


Figure 1.32 b Decorana ordination of Group 2 samples on first two axes.

and Temora and were also associated with higher abundances of Rotifera. Rotifera, harpacticid copepods and Eurytemora occurred abundantly in all samples. At level 3, groups 1 to 4 were predominantly Skinflats, Dunmore and Kincardine (Culross was not sampled until March 1982), while 5 to 8 were biased towards Dunmore, S.Alloa and Fallin (Fig.1.32a). Groups 5 and 6 were mainly high tide samples, while 7 and 8 were mainly low tide samples.

F-ratios were significant for Dist, Inorg, Sal, and Temp (Table 1.10) Dist was associated with function 1 and the remaining variables with function 2 (Table 1.11a). MDA accounted for 98.1% of variance, and 100% of samples were correctly reclassified (Table 1.11b). The environmental data set was not sufficiently complete to permit interpretation in detail for this sample group.

Date Group 3 (March/April 1982)

This group consisted of 39 samples.

DCA axis 1 indicated considerably greater species turnover than axis 2 (Fig.1.33b). Dist, Tide, Xorg, Sal and Temp were correlated with axis 1, and Inorg and Org with axis 2 (Table 1.14).

Dispersion on axis 2 decreased with increasing value of axis 1 scores.

Eurytemora, harpacticids, Rotifera and Maranzelleria occurred in almost all samples, and Littorina egg capsules and cirripede nauplii in the majority (Table 1.22). The major level 1 TS division was very uneven, and 7 groups were defined at level three.

Maranzelleria was the indicator for one side of the division, and Diaptomus and Bosmina the indicators for the other. Group 1 at level three was characterised by Sagitta, Oithona, Calanus, Temora, Pseudocalanus and Littorina veligers. Maranzelleria trochophores and eggs were diagnostic of group 2, the majority of samples in which also contained Oithona and Temora. Group 3 was rather indifferent, containing samples with relatively few taxa but particularly with a reduced frequency and abundance of Maranzelleria eggs. Group 3 was also characterised by the highest abundances of Eurytemora. The majority of samples in group 4 contained Oithona, Temora, Acartia bifilosa inermis, Pseudocalanus, and Littorina veligers. The remaining three groups contained samples devoid of neritic copepods, with a much reduced frequency of Maranzelleria, cirripede nauplii and Littorina egg capsules and with the majority of occurrences of Daphnia, Bosmina and Diaptomus.

The dendrogram displayed considerable sorting of samples by tide. Group 1 consisted of high spring tide samples and group 2 predominantly so. Group 3 contained mixed neap tide samples, group 4 high neap samples, groups 5 and 6 mostly low tide samples and group 7 low spring tide samples. As with date group 2, there was also a clear bias towards lower-estuary stations in groups

1-4, and to upper estuary stations in groups 5-7.

Dist, Tide, %org, Phaeo, AR and Sal all had significant F-ratios (Table 1.10). Sal, Dist, Tide and %org were associated with MDA function 1 and AR with function 2 (Table 1.11a). 84.9% of the variance was explained by the first two discriminant functions, and 85% of samples were correctly reclassified (Table 1.11b). The sorting of samples described above was well-represented by the clustering in discriminant space of groups defined by level 2 TS analysis (Fig.1.33c3 c.)

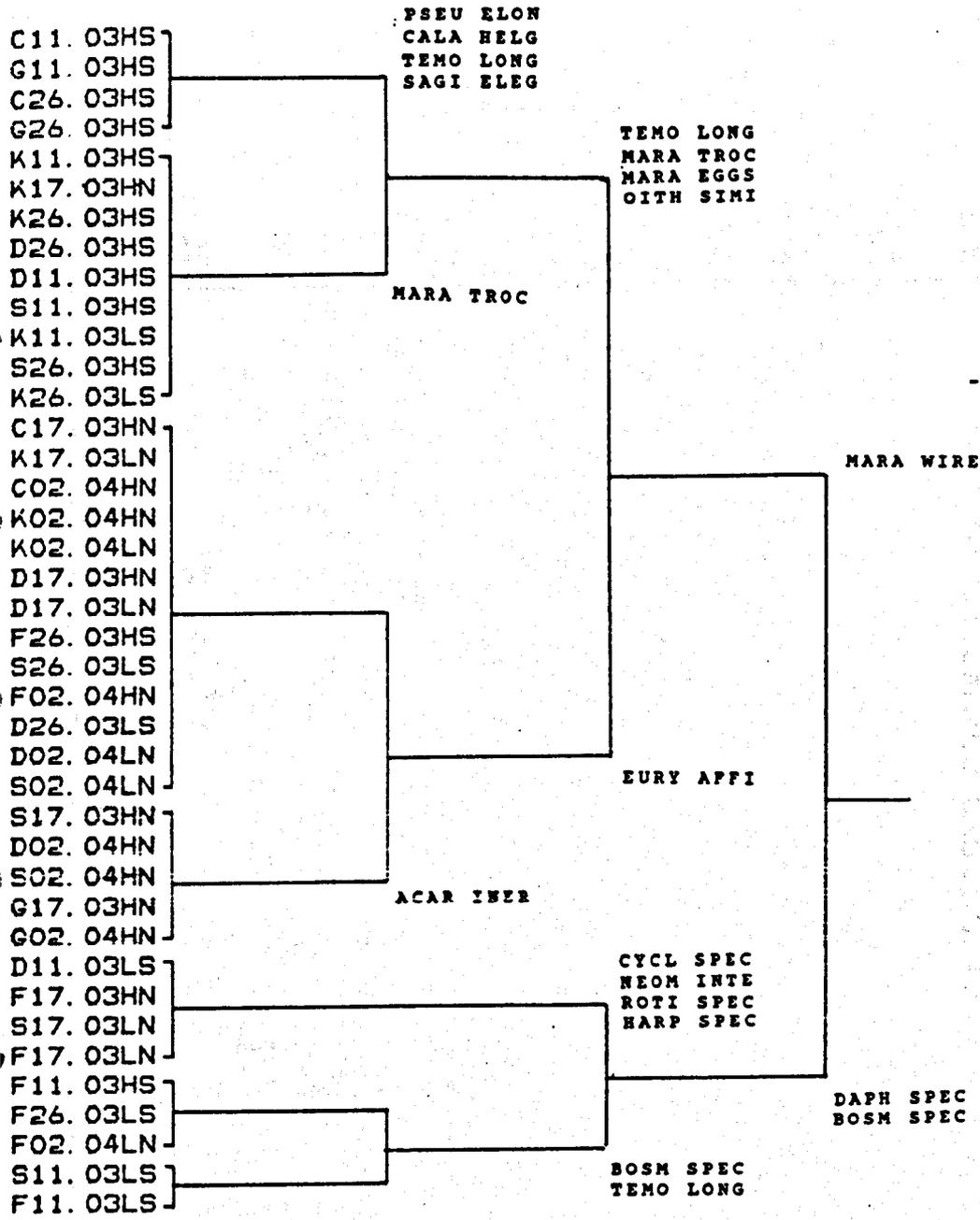
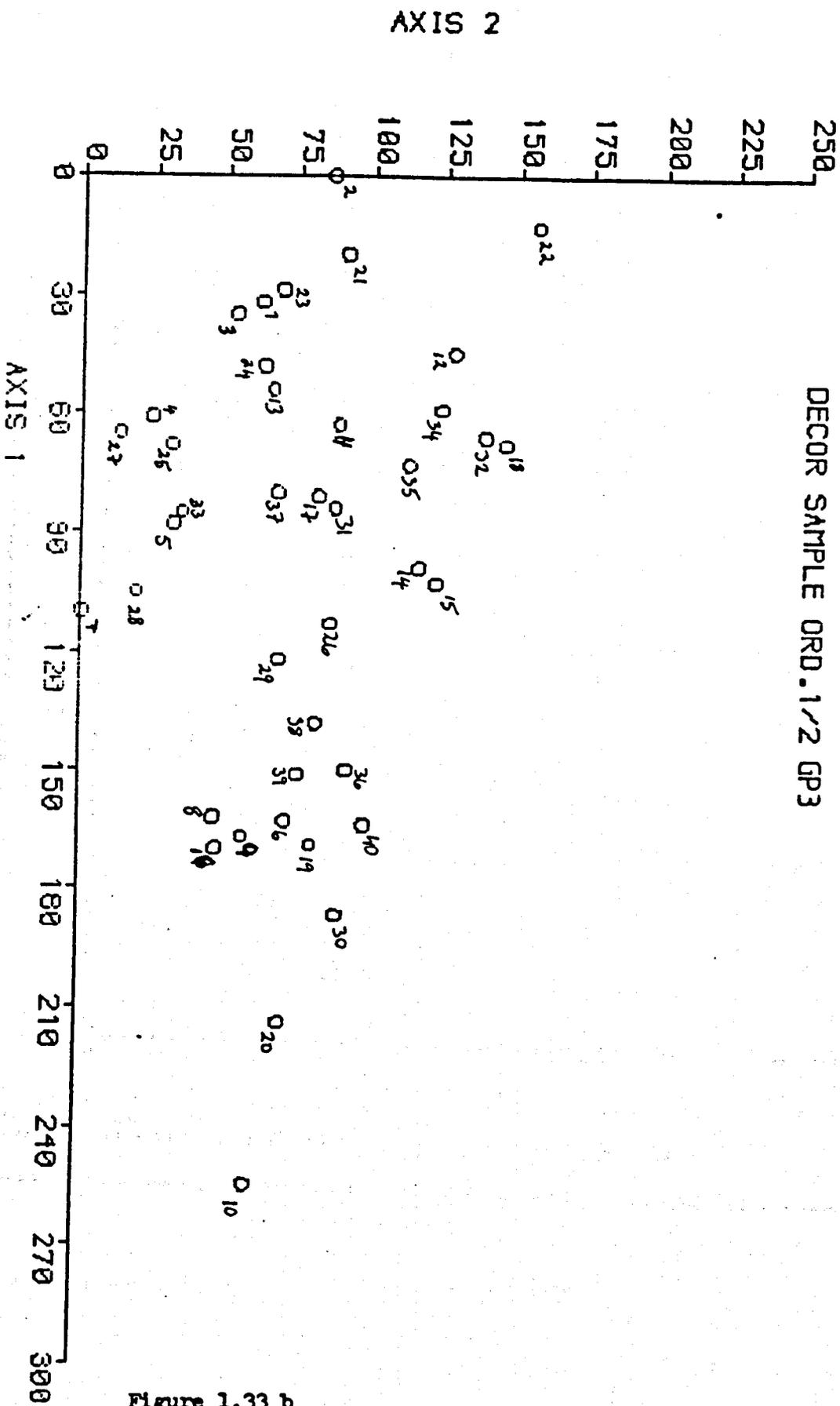


Figure 1.33 a

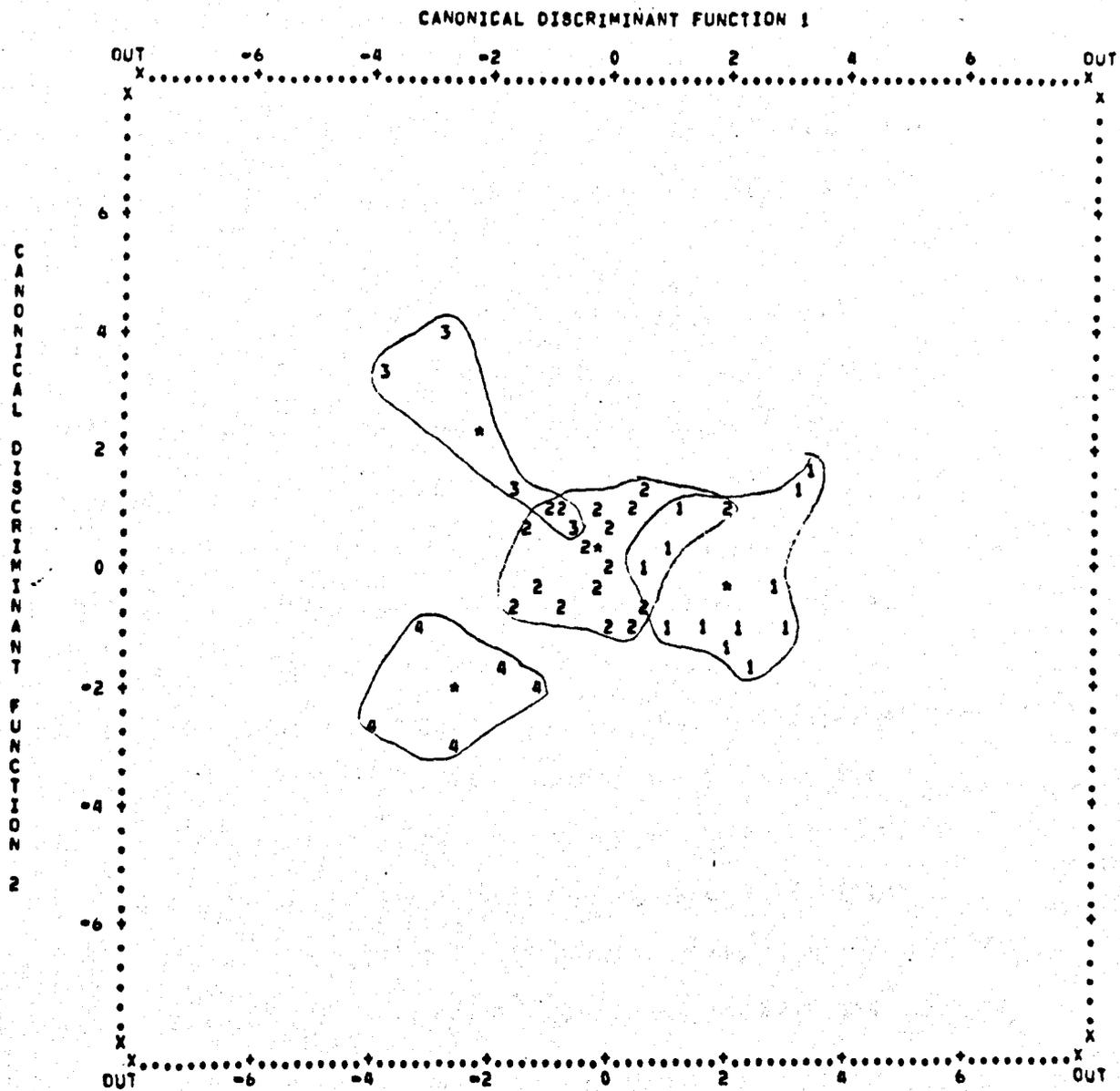
Dendrogram of Group 3 samples classified by Twinspan. Indicator species for each division shown.



DECOR SAMPLE ORD. 1/2 GP3

Figure 1.33 b

Decorana ordination of Group3 samples on first two axes.



4-DEC-84
14:43:55

MDA GP3 TS
UNIVERSITY OF STIRLING

DEC VAX-11/780 VMS V3.6

Figure 1.33 c MDA: Group 3

Date group 4 (May 1982)

Group 4 contained 39 samples.

DCA axis 1 represented greater taxonomic diversity than axis 2 (Fig.1.34b). Dist, Tide, % org, Sal, Temp, Inor, Ar and Phaeo were correlated with axis 1; no variable was significantly correlated with axis 2 (Table 1.14)4.

The major TS division (Table 1.23) was characterised by high Eurytemora abundance on one side and Centropages, Polydora and terebellid larvae and cirripede nauplii on the other. A large number of marine and neritic copepod species and additional meroplanktonic larvae also occurred in this latter group.

Freshwater taxa were barely represented in May samples. Samples were classified at TS level three primarily into lower estuary/high tide samples (groups 1-4) versus upper estuary/low tide samples (groups 5-8) (Fig.1.34a). There was a tendency for the frequency of neap tide samples to increase from group 1 to 8.

Dist, Tide, %org, Phaeo, AR and Sal all had significant F-ratios (Table 1.10). MDA was carried out on TS level 2 classification (four groups). Sal was associated with function 1, and Dist and Tide with function 2 (Table 1.11a). 98.5% of variance was accounted for by the first two discriminant functions, and 86.2% of samples were correctly reclassified (Table 1.11b). Discrimination on function 2 was not good, but the correct order of groups was recovered on function 1 (Fig.1.34c)34c.

Table 1.23 Twinspan classification of Date Group 4 samples

GP4

	1	123	2232	23	33113	1222	233	113231	11	
	231001	12234543	216344	766786557	5989979	808				
8 ACAR CLAU	-----	2-----	-----	-----	-----	-----	-----	-----	-----	00000
21 PARA PARV	-----	12-----	-----	-----	-----	-----	-----	-----	-----	00000
23 SAGI ELEG	-----	1-21-----	-----	-----	-----	-----	-----	-----	-----	00000
35 SYLL SPEC	-----	1-1-----	-----	-----	-----	-----	-----	-----	-----	00000
16 PSEU ELON	-----	21233121	-----	-----	-----	-----	-----	-----	-----	00001
17 OITH SIMI	1-2-32	-321121	-----	-----	-----	-----	-----	-----	-----	0001
19 CALA HELG	-----	1-1-1-----	-----	-----	-----	-----	-----	-----	-----	0001
20 TEMO LONG	11-1123	2233121	-----	-----	-----	-----	-----	-----	-----	0001
9 ACAR LONG	-----	231-2-----	-----	-----	-----	-----	-----	-----	-----	001
18 CENT HAMA	11-123	1133232	2222-1	-----	-----	-----	-----	-----	-----	001
12 ACAR INER	3-2-243	-21-1112	-----	-----	-----	-----	-----	-----	-----	0100
33 LITT VELI	2-31-23	-2-111-----	-----	-----	-----	-----	-----	-----	-----	0100
37 TERE LARV	221223	1222111	-----	-----	-----	-----	-----	-----	-----	0100
40 CIRR NAUP	3333343	3232112	-----	-----	-----	-----	-----	-----	-----	0100
32 LITT CAPS	224441	-1-1-1-11	-----	-----	-----	-----	-----	-----	-----	0101
42 NUDI JUVE	2-2-2	-----	-----	-----	-----	-----	-----	-----	-----	0101
28 POLY CILI	433324	43533233	223222	-----	-----	-----	-----	-----	-----	011
39 CIRR CYPR	212113	22233112	-----	-----	-----	-----	-----	-----	-----	011
38 NERE LARV	21-11	-2221232	-----	-----	-----	-----	-----	-----	-----	100
41 BIVA LARV	-----	11-----	-----	-----	-----	-----	-----	-----	-----	100
26 ROTI SPEC	21-----	4-322522	-----	-----	-----	-----	-----	-----	-----	101
34 APHR LARV	1-----	1-----	-----	-----	-----	-----	-----	-----	-----	101
36 ETEO LARV	-----	1-1-----	-----	-----	-----	-----	-----	-----	-----	101
2 BOSM SPEC	-----	-----	-----	-----	-----	-----	-----	-----	-----	1100
3 DIAP GRAC	-----	-----	-----	-----	-----	-----	-----	-----	-----	1100
4 NEOM INTE	-----	-----	-----	-----	-----	-----	-----	-----	-----	1100
5 EURY AFFI	432323	44354554	324555	-----	-----	-----	-----	-----	-----	1101
22 CYCL SPEC	-----	-----	-----	-----	-----	-----	-----	-----	-----	1101
29 MARA WIRE	-----	-----	-----	-----	-----	-----	-----	-----	-----	1101
27 HARP SPEC	133233	42122223	454212	-----	-----	-----	-----	-----	-----	111
	000000	00000000	000111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	
	000000	11111111	111000	0000000000	1111111111	1111111111	1111111111	1111111111	1111111111	
	011111	10000000	111000	1111111111	10000000	1111111111	10000000	1111111111	1111111111	
	00001000	111111		0001111111	10000001					
		011111		0011111000001						
				001111000001						
				00011						

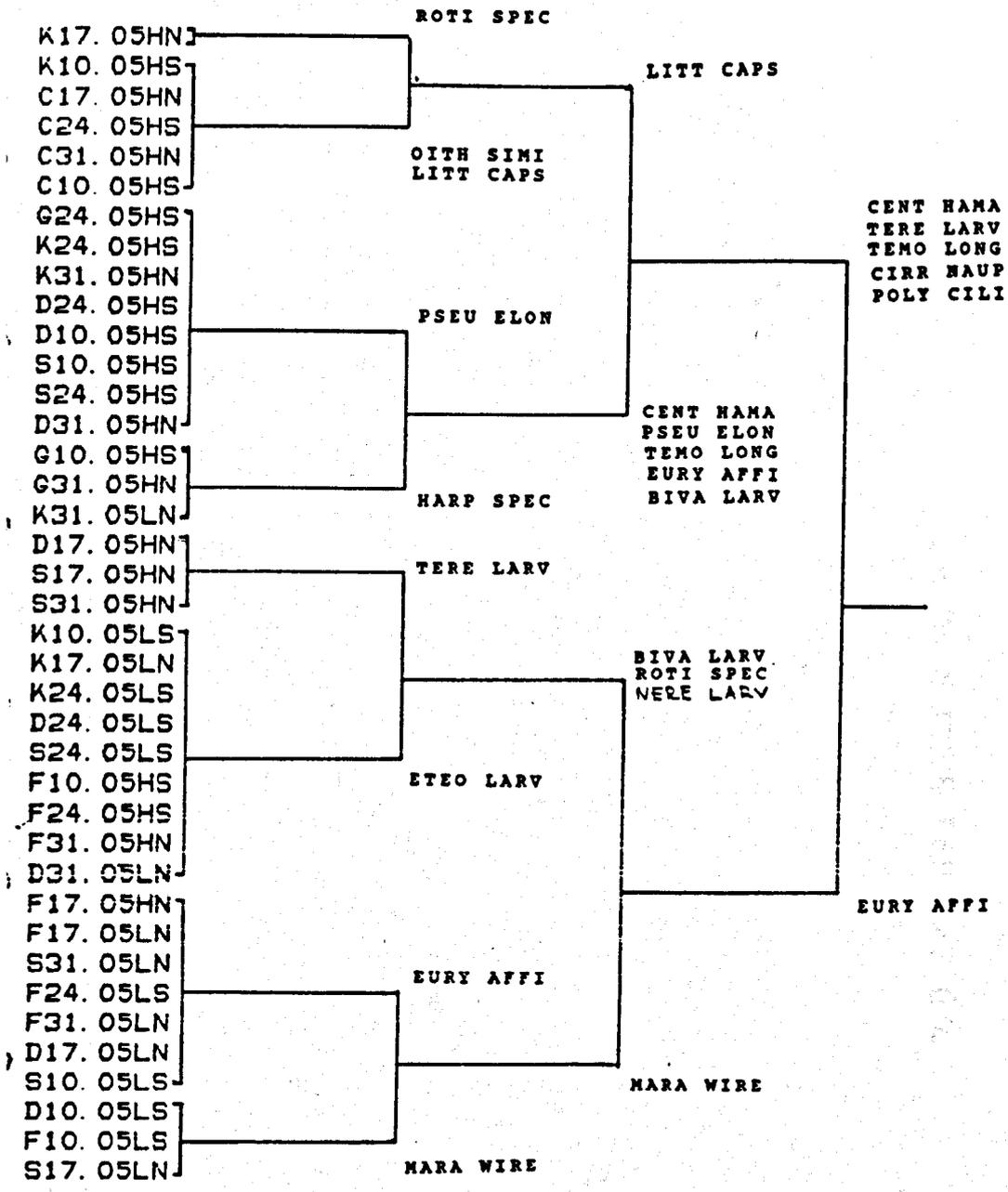
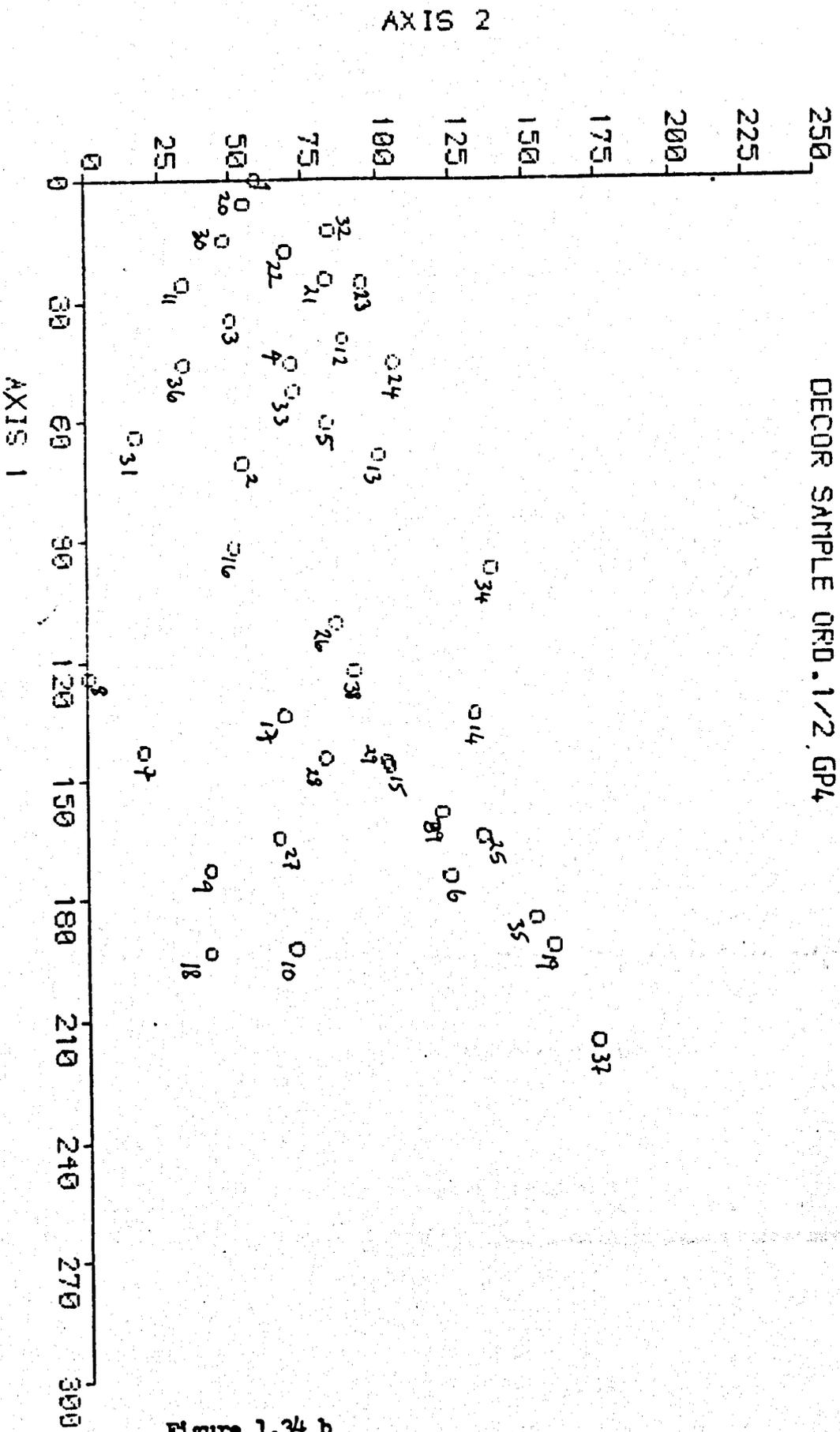


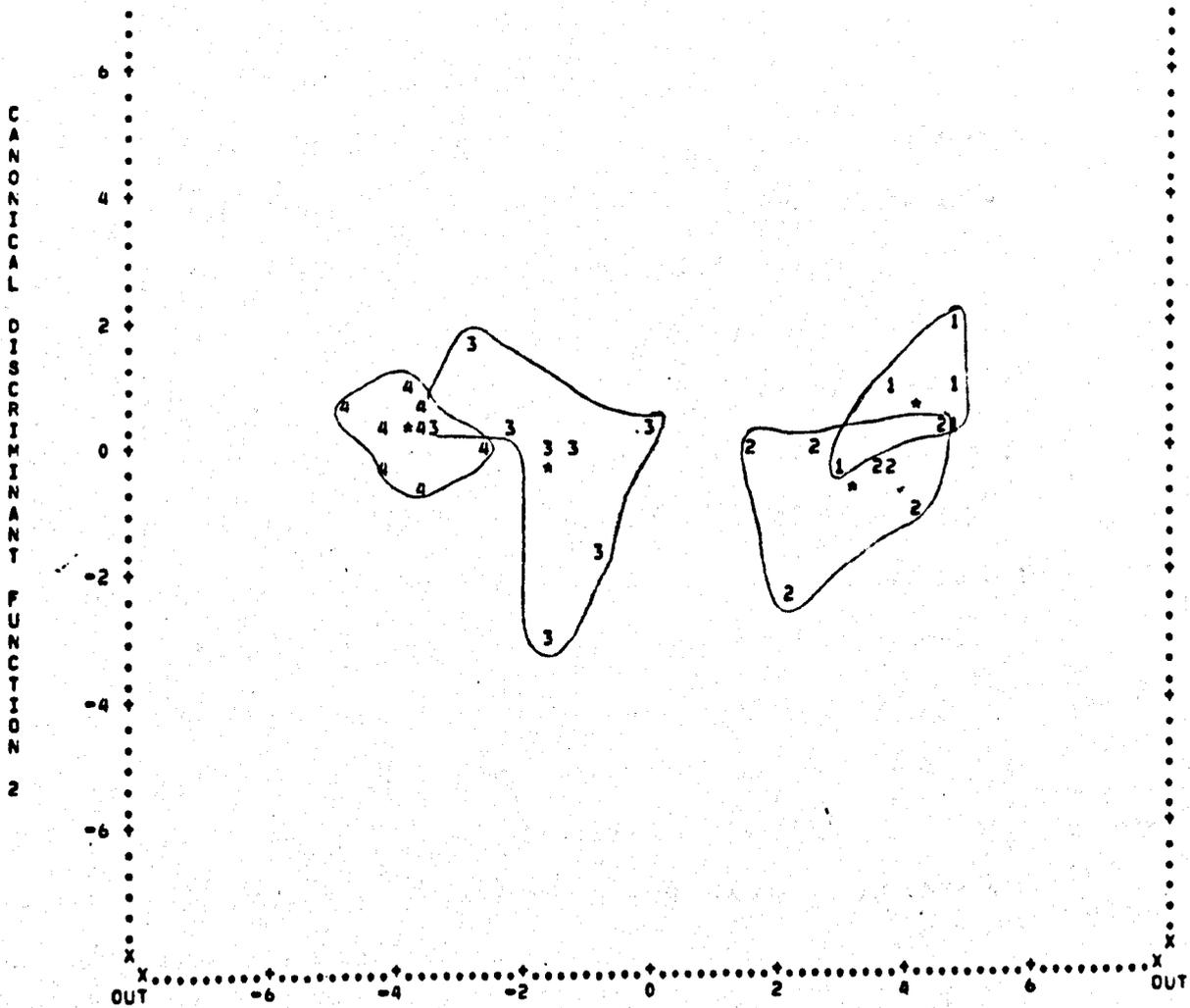
Figure 1.34 a

Dendrogram of Group 4 samples classified by Twinspan. Indicator species for each division shown.



DECOR SAMPLE ORD. 1/2. GP4

Figure 1.34 b
Decorana ordination of Group4 samples on first two axes.



4-DEC-84
14:50:52

MDA GP4 TS
UNIVERSITY OF STIRLING

DEC VAX-11/780 VMS V3.6

CLASSIFICATION RESULTS -

ACTUAL GROUP	NO. OF CASES	PREDICTED GROUP MEMBERSHIP			
		1	2	3	4

Figure 1.34 c MDA: Group 4

Date Group 7 (September 1982)

Date group 7 contained 39 samples.

DCA ordination showed that axis 1 was considerably stronger than axis 2 (Fig.1.35b), with some indication of a cluster at low axis 1 scores. All variables except Chla , AR and Disch were significantly correlated with axis 1, and none with axis 2.

The major level 1 division in TS classification corresponds to the DCA ordination (Table 1.24), with level three groups 1,2,3 and 4 matching the cluster noted above. The pattern of tidal sorting of samples (Fig.1.35a) corresponded closely to that observed in Date group 4; The frequency of marine/neritic taxa and meroplanktonic larvae declined from group 1 to 4, with only A.tonsa, Polydora larvae, and cirripede nauplii being represented in groups 5-8. Groups 5-8 were characterised by increased frequency of occurrence of Rotifera and the presence of freshwater taxa absent from groups 1-4.

MDA was conducted on TS level 2 classification (four groups). All variables except Chla had significant F-ratios (Table 1.10). Sal, Dist, %org and tide were associated with function 1, and Inor, Phaeo, and AR were associated with function 2 (Table). 97.5% of the variance was explained by the first two discriminant functions (Table 1.11b). and 91.7% of samples were correctly reclassified (Table 1.11b). Groups 1-4 (TS 1/2.3/4,5/6,7/8) were

Table 1.24 Twinspan classification of Date Group 7 samples

GP7

	22	2111	1122	123	13122	333112332	
	1301	22136	02894	5451	773834	825659704609	
32 L111 CAPS	1-22	-----	-----	-----	-----	-----11-----	0000
21 PARA PARV	---1	-----	-----	-----	-----	-----	00010
24 OIKO DIOI	3322	-2-----	-----	-1-----	-----	-----	00010
36 EIEO LARV	-2---	-----	-----	-----	-----	-----	00010
42 NUDI JUVE	---1	-----	-----	-----	-----	-----	00010
20 TEMO LONG	11-211	---1-----	-----	-----	-----	-----	00011
23 SAGI ELEG	-1-111	-----	-----	-----	-----	-----	00011
16 PSEU ELON	11121	-11-----	-----1	-----	-----	-----1-	001
17 OITH SIMI	232322	21111-11	-1-----	-----	-----	-----	001
18 CENT HAMA	-----	-1-1-----	-----	-----	-----	-----	001
8 ACAR CLAU	-----	22-----	-----	-----1	-----	-----	0100
9 ACAR LONG	211--	23221---	-----	-1----1	-----	-----1-	0100
41 GIVA LARV	-----	-1-1-----	-----	-----	-----	-----	0100
28 POLY CILI	-42322	1-122121	2121	2121	-----	-----1-	0101
40 CIRR NAUP	344222	21-33122	-221212	--1	-----	-----	0101
39 CIRR CYPR	232212	2-1-2--1	-----	-----11	-----	-----2-	011
10 ACAR TONS	122323	2211---3	322-221	122	---1-----	-----	10
27 HARP SPEC	3233--	222221-1	-111231	-222-111	-212211		10
4 NEOM INTE	-----	2-12-----	-----	21311	-1-211-11	22	110
5 EURY AFFI	2-1212	12211-2	-333323	224322	22222223	21	110
1 DAPH SPEC	-----	-----	-----	1-----	-----	-----1	1110
2 BOSM SPEC	-----	-----	-----	-1111	-----111-11	-----2	1110
26 ROTI SPEC	-----	2-----	-----	2222	--2332121222	-121-	1110
34 APHR LARV	-----	-----	-----	-----	-----1	-----	1110
3 DIAP GRAC	-----	-----	-----	-1-1	-----31-1	-----	1111
12 ACAR INER	-----	-----	-----	-----	-----	-----1-	1111
15 CHYD SPEC	-----	-----	-----	-----	2--1-11	--212	1111
22 CYCL SPEC	-----	-----	-----	-1-----	1111	-----211	1111
	0000	00000	00000	1111	1111111	111111111111	11
	0000	00111	11111	0000	000000	111111111111	11
	0000	11000	11111	0000	111111	0000000000	11
			00001		000111	0000111111	
						000001	
						00011	

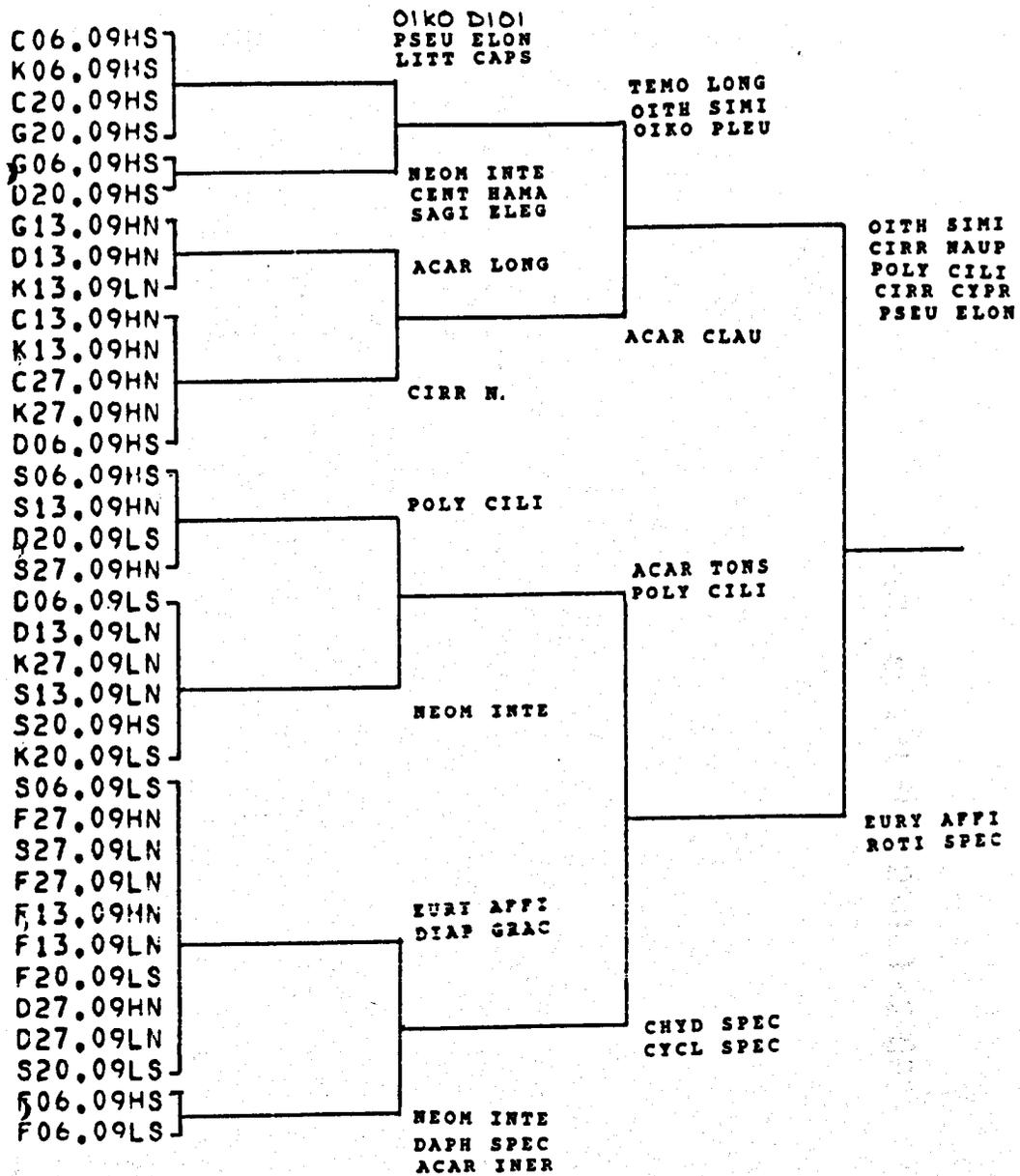


Figure 1.35 a

Dendrogram of Group 7 samples classified by Twinspan. Indicator species for each division shown.

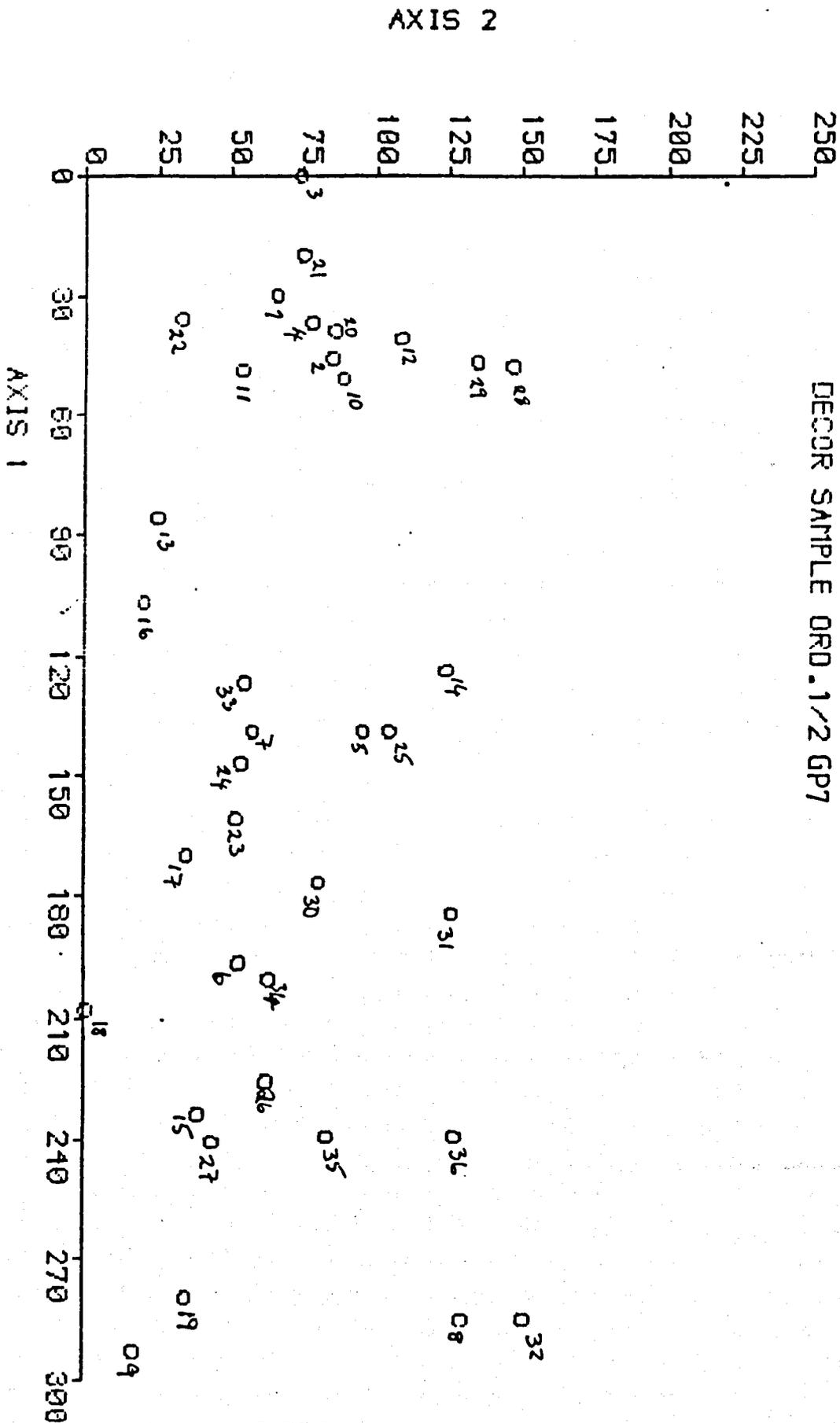
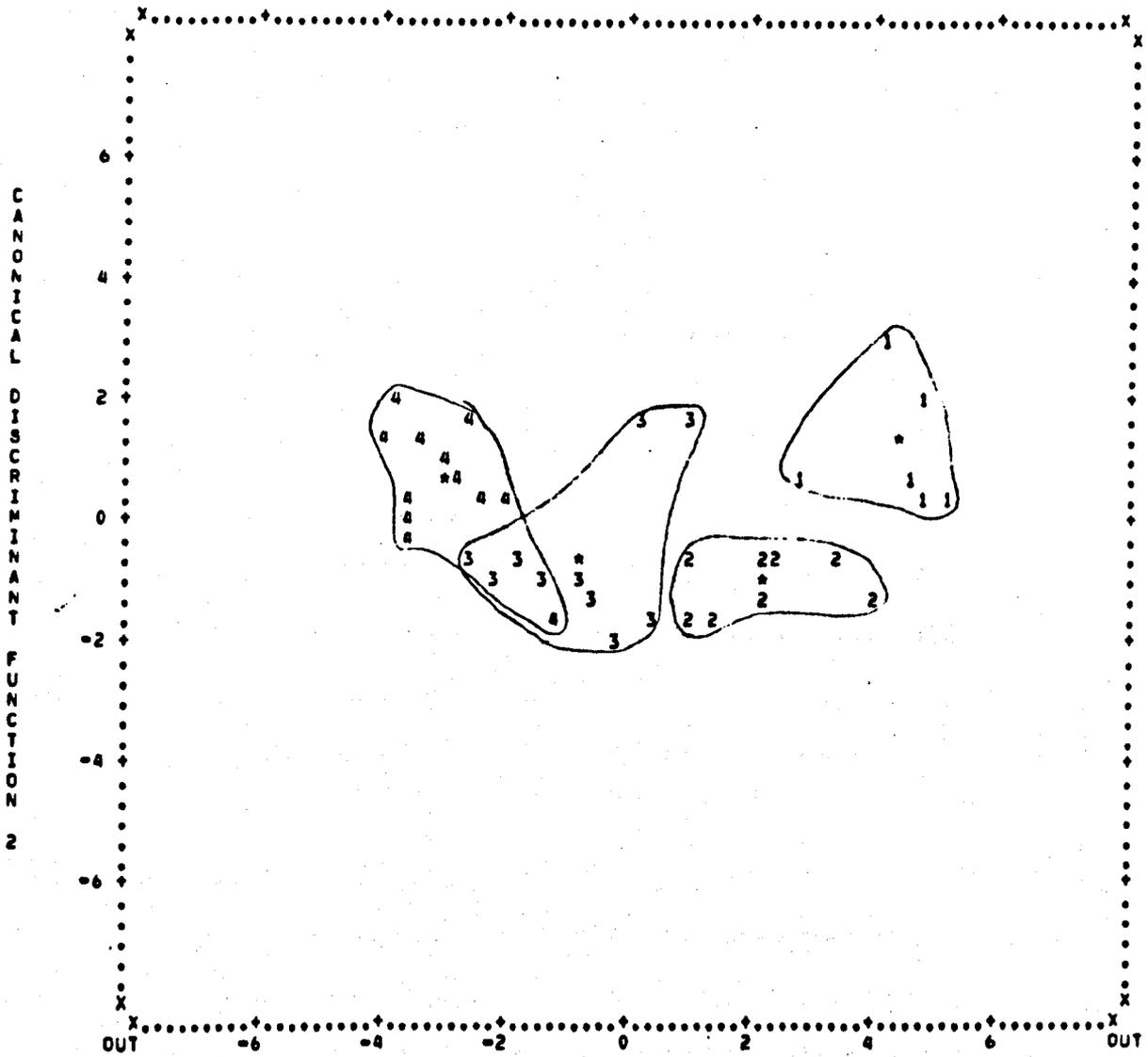


Figure 1.35 b

Decorana ordination of Group 7 samples on first two axes.



4-DEC-84
15100128

MDA GP7 TS
UNIVERSITY OF STIRLING

DEC VAX-11/780 VMS V3.6

CLASSIFICATION RESULTS -

Figure 1.35 c MDA Group 7

correctly ordered on the first discriminant axis (Fig.1.35c). TS 1/2 (lower estuary, high spring tides) were separated from TS 3/4 on axis 2 by virtue of lower inorganic suspended solids, lower phaeopigments, and a more viable phytoplankton population.

Date Group 8 (November 1982)

This group contained 36 samples.

DCA sample scores were more dispersed on axis 1 than on axis 2 (Fig.1.36b), with a tight cluster at an axis 1 score of about 150. Only Dist, Tide and Sal were significantly correlated with axis 1, and no variables were significantly correlated with axis 2 (Table 1.14).

TS classification was carried to level 3. Temora was the indicator for one side of the major division, and Diaptomus and Neomysis for the other. Neomysis was the only frequently-occurring species in groups 4-6; freshwater taxa were only sparsely represented in this sample set. Group 1 was notable for the co-occurrence of five of the 6 Acartia species present in the Forth, and also contained samples with Oikopleura and Sagitta. Temora, Pseudocalanus, Oithona and cirripede nauplii were present in almost all samples in groups 1-3. Group 2 was distinguished from groups 1 and 3 primarily by the absence of

A.tonsa and A.bifilosa inermis. Samples were again clearly sorted by tide in the classification (Fig.1.36a); 1-3 were mainly high tide and Kincardine, Culross and Skinflats, while 4-6 were mainly low tides and Fallin, S.Alloa and Dunmore.

MDA was carried out on four groups defined by TS at level 2. Dist, Tide, Inorg, Org, Phaeo and Sal had significant F-ratios (Table 1.10). Sal and Dist were associated with function 1 (Table 1.11a) and Phaeo and Inor with function 2. 96.7% of the variance was explained by the first two discriminant functions, and 97.2% of samples were successfully reclassified (Table 1.11b). The sample groups were clearly distinguished in discriminant space (Fig.1.36c) on function 1 in terms of salinity and distance from upper tidal limit. Little intelligible discrimination was apparent on function 2.

Table 1.25 Twinspan classification of Date Group 8 samples

GP8

	13	122	122	123	1333	122	1	223	12	113	
	1311	2294	3032	0106	2468	7878	956	565	574	493	
13 ACAR DISC	3-1										0000
18 CENT HAMA	-4										0000
24 OIKO DIOI	222	-1		1-1							0000
33 LITT VELI	---	1									0000
8 ACAR CLAU	1121	-1		-2-1							0001
32 LITT CAPS	1			-1							0001
10 ACAR TONS	2322	---	2-1	12-1							00100
12 ACAR INER	2222	---	1-1	2211				-1			00100
19 CALA HELG	---	1		-11							00101
20 TEMO LONG	2232	111	1111	1212							00101
23 SAGI ELEG	1-2			1111							00101
11 ACAR BIFI	---	1									0011
28 POLY CILI	11-1	211									0011
42 NUDI JUVE	---			-1							0011
9 ACAR LONG	2232	1	111	---	111						01
16 PSEU ELON	3343	212	2232	3242	1-11			-2			01
17 OITH SIMI	3333	132	2222	322-	2-2				1111	-1	01
40 CIRR NAUP	2211	212	1111	221-	1				-11		01
5 EURY AFFI	3433	2214	4444	4243	3433	2332	2222	3352	444	314	10
27 HARP SPEC	2222	-23	2123	3323	1221	321	-222	2343	122	---	10
26 ROTI SPEC	3-4	1-3	23-3	422-	2222	222-	2223	344	245	324	110
34 APHR LARV	---							-1			11100
41 BIVA LARV	---							-1			11100
2 BOSM SPEC	---					1-1					11101
4 NEOM INTE	---		1		2212	2211	1-1	2122	-2		11101
15 CHYD SPEC	---						-2			11	11101
1 DAPH SPEC	---				1	1				11	1111
3 DIAP GRAC	-1				-2	11		-2	-1	-22	1111
22 CYCL SPEC	---							1-1		-21	1111
	0000	000	0000	0000	1111	1111111	11111	1111	111	111	
	0000	1111	1111	1111	0000	0000000	0000	000	000	111	
		000	1111	1111	0000	0000000	1111	111			
		0000	1111	0000	1111111	0000	111				
					0001111						

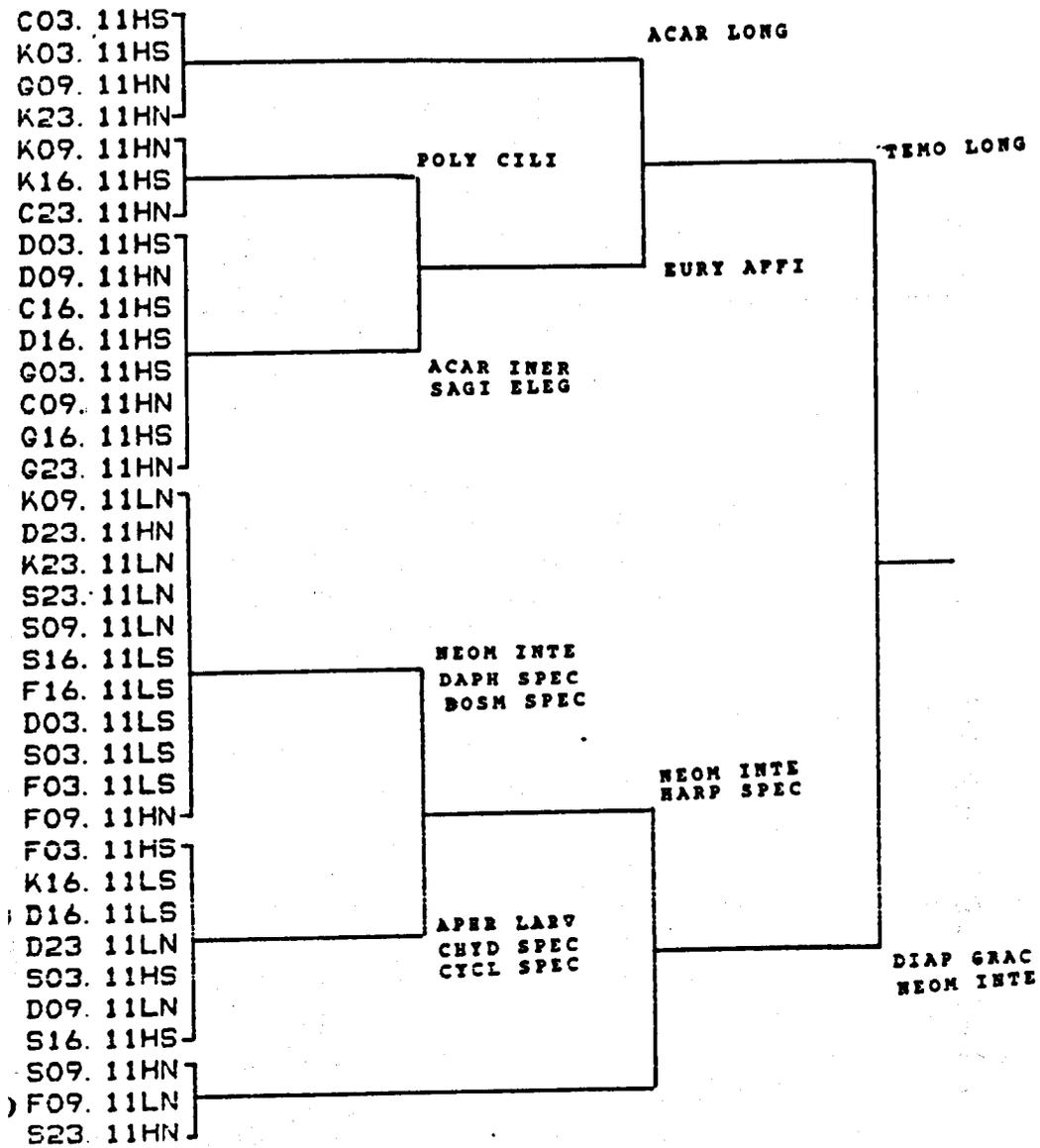
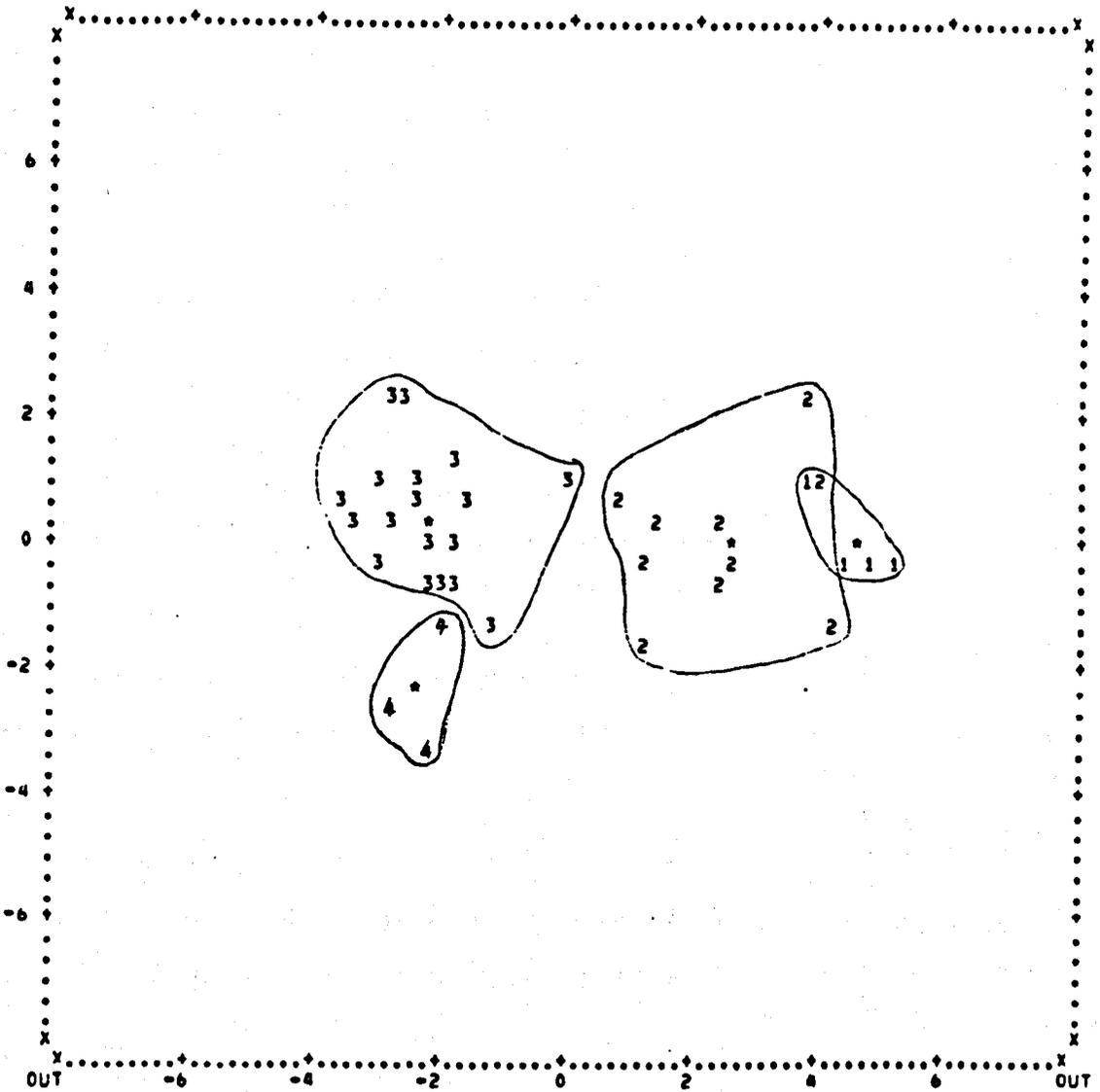


Figure 1.36 a

Dendrogram of Group 8 samples classified by Twinspan. Indicator species for each division shown.

CANONICAL DISCRIMINANT FUNCTION



4-DEC-84
15:37:50

MDA GPA TS
UNIVERSITY OF STIRLING

DEC VAX-11/780 VMS V3.6

CLASSIFICATION RESULTS -

Figure 1.36 c MDA: Group 8

Tidal state (High, Low, Spring, Neap etc.)

Correlations between DCA axis scores and environmental variables are summarised in Table 1.12. As with other sample categories, axis 1 was most strongly related to most variables, especially to Dist, Sal, and Temp. Suspended particulate characteristics were most strongly related to axis scores in the high spring tide category. On axis 2, Date was the most consistently correlated variable. Chla was most strongly correlated with axis scores in the low Spring tide category.

Between 71.5% and 93.6% of variance was accounted for by the first two discriminant functions (Table 1.11b), and between 70.3% and 90.9% of samples were correctly reclassified (Table 1.11b). Function 1 invariably accounted for more variance than function 2; the difference was least in the Spring tide category and greatest in the Low spring tide category. Of the variables considered, only Inorg, Org, and Phaeo did not have significant F-ratios for the majority of categories (Table 1.10). With the exception of the High spring and Low spring categories, Sal and Dist were the most influential variables on MDA function 1 (Table 1.11a). Date and Disch were most consistently associated with function 2.

Variables were projected onto discriminant space for all-sample, high, low, spring, and neap categories; further subdivision of tidal state did not recover additional useful information. For the purposes of vector projection, variables have been labelled as follows:

- a Distance from upper tidal limit
- b Date (decimal)
- c Discharge of freshwater into the estuary
- d Inorganic suspended solids
- e Organic content of suspended solids
- f Chlorophyll a
- g Phaeopigments
- h Acid ratio
- i Salinity
- j Temperature
- k Tidal state

High tide

The TS indicators for the major level 1 division were Rotifera on one side versus Polydora, cirripede nauplii, Temora, Oithona and Pseudocalanus on the other (Table 1.26). Maranzelleria forms created a distinct cluster of samples which formed groups 5 and 6 at level three, as did the freshwater taxa Daphnia, Bosmina and Diaptomus in group 8. Group 1 was a singleton with very few taxa present except Neomysis in high abundance. Indicators for group 3 were terebellid larvae, Centropages, cirripede cyprids, nereid larvae and bivalve larvae (Fig.1.37); this group also contained many neritic and marine taxa which occurred in other groups. Group 4 was distinguished from 3 primarily by the absence of terebellid larvae, Centropages and cirripede cyprids. Littorina capsules and veligers were also less common in group 4 than 3; while both groups had a high frequency of high spring tides, group 3 was identifiable as comprising samples collected in the spring, and group 4 was predominantly composed of samples taken in November and December.

MDA (Fig.1.41a, Table 1.11a) shows Date, Dist and Sal vectors most influential, with TS groups 1, 2, 3 and 4 (at level three) separated from 5, 6, 7 and 8 on the basis of Dist and Sal, and 3/4 separated from 5/6 on the basis of date.

1, 2 and 4 showed some small positive influence of Chla, AR and Temp, while 3 was associated with %org to a greater extent than

other groups. Group 3 indicated the association of larval forms and Temora with lower-estuary, higher-salinity conditions, while group 4, with a strong Pseudocalanus/Oithona association was linked to later dates and rather lower salinity.

In contrast, Groups 5-8 were associated with a range of dates, tending to later dates from 5 to 8 but also to lower salinities and increased dominance of freshwater taxa. Group 8 showed little date preference, but a very strong tendency to low salinity.

Groups 2 and 3 were more strongly influenced than other groups by all variables except Date; 5 and 6 included almost all samples from the third date group and none from any other date group and were, as noted above, characterised by Maranzelleria.

The variables of minor influence (e,f,h,j) all tended in the same direction as Sal and Dist.

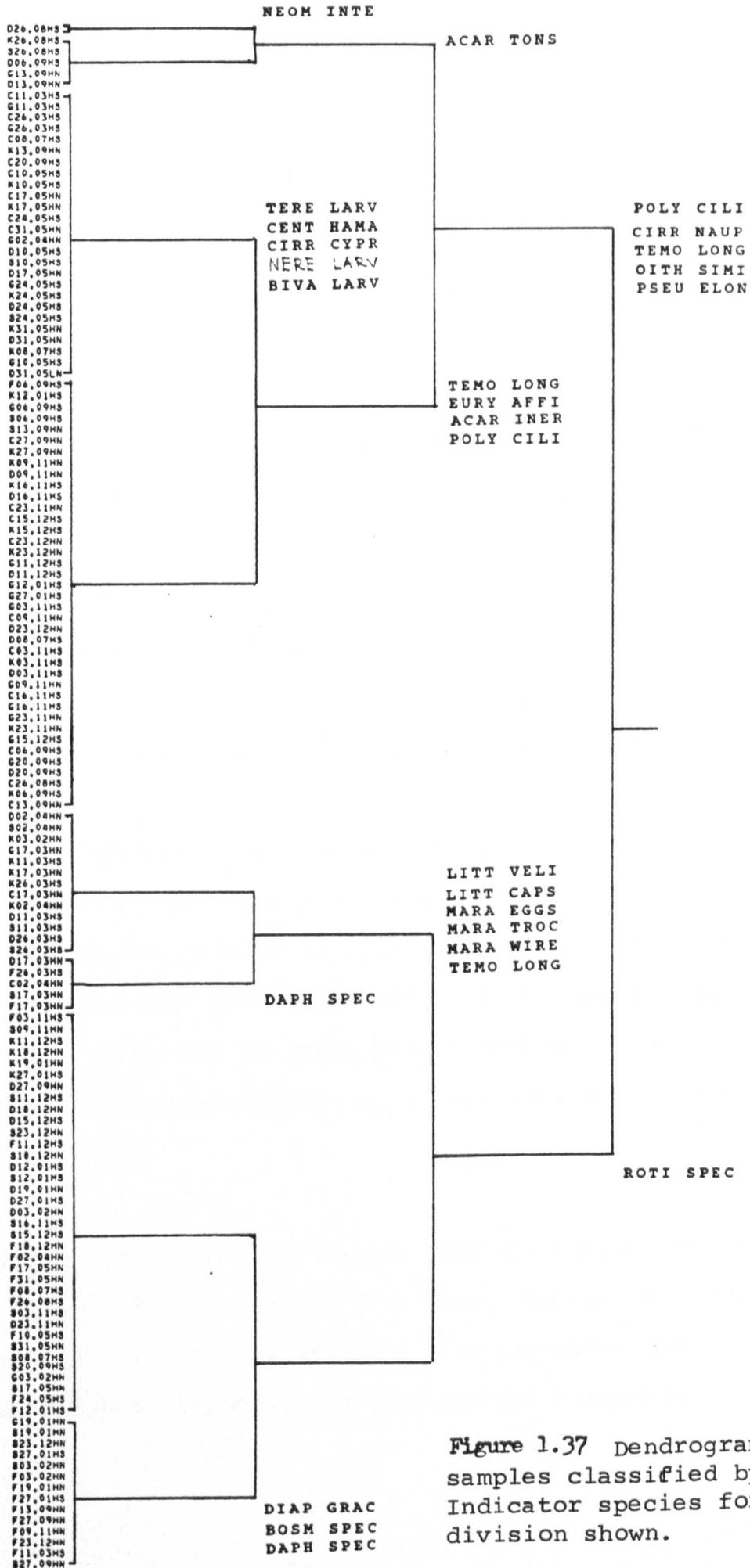


Figure 1.37 dendrogram of High tide samples classified by Twinspan. Indicator species for each division shown.

Low tide

TS and MDA analyses were carried out to division level three (eight groups).

Indicators for the major division were cirripede nauplii and Oithona versus freshwater chydorids and cladocera. Group 1 was composed of samples with joint occurrence of Maranzelleria stages. Group 2 was rather sparse of species and was dominated by high abundance of Eurytemora (Table 1.27). Group 3 contained a considerable number of larval orms (Eteone, Nereis, bivalves, Polydora) but differed from group 2 by virtue of high rotifer abundance. Group 4 included the majority of occurrences of cirripede nauplii, Oithona and A.tonsa, but only isolated occurrences of the larval forms common in group 3.

Groups 5-8 were characterised by the almost complete absence of the neritic copepods and benthic larval forms, and by increasing (from 5 to 8) frequency of occurrence of freshwater taxa. Chydorids and cyclopids were, however, largely confined to group 6.

The sample sequence (Fig.1.38) showed evidence of strong selection for date in groups 1 and 2. Groups 3 and 4 consisted almost entirely of Kincardine and Dunmore samples and differed considerably in date. Group 5 covered the same time period as 4, but included more S.Alloa samples, while 6 again covered the same general time period as 4 and 5 but included more Fallin samples. Groups 7 and 8 were mainly winter samples, and 8 had the highest relative frequency of Fallin samples.

The MDA plot showed, as with high tide samples, that 1,2,3 and 4 were clearly separated from 5,6,7 and 8 on the basis of Dist. Disch, and Sal; the former set of groups had higher salinity and the latter were associated with higher freshwater discharge. The effects of discharge and distance in

distinguishing 4 and 5 can be seen by comparing their taxonomic composition; group 4 (with the majority of September samples) with lower discharge and greater distance from upper tidal limit contained more meroplanktonic larvae, while group 5 contained samples dominated by the more persistent upper-estuary forms Eurytemora, Rotifera and harpacticids. Group 4 was also associated with higher Chla values.

Temp and %org were influential in the same direction as Sal and Dist, but Phaeo was more closely linked to Date and Disch. The MDA plot correctly indicated that groups 1,2,3,7 and 8 were distinguished from 4,5 and 6 by Date.

A considerable amount of community structure was revealed, despite the fact that 20 out of 88 samples were excluded from the analysis due to incompleteness of the environmental data set.

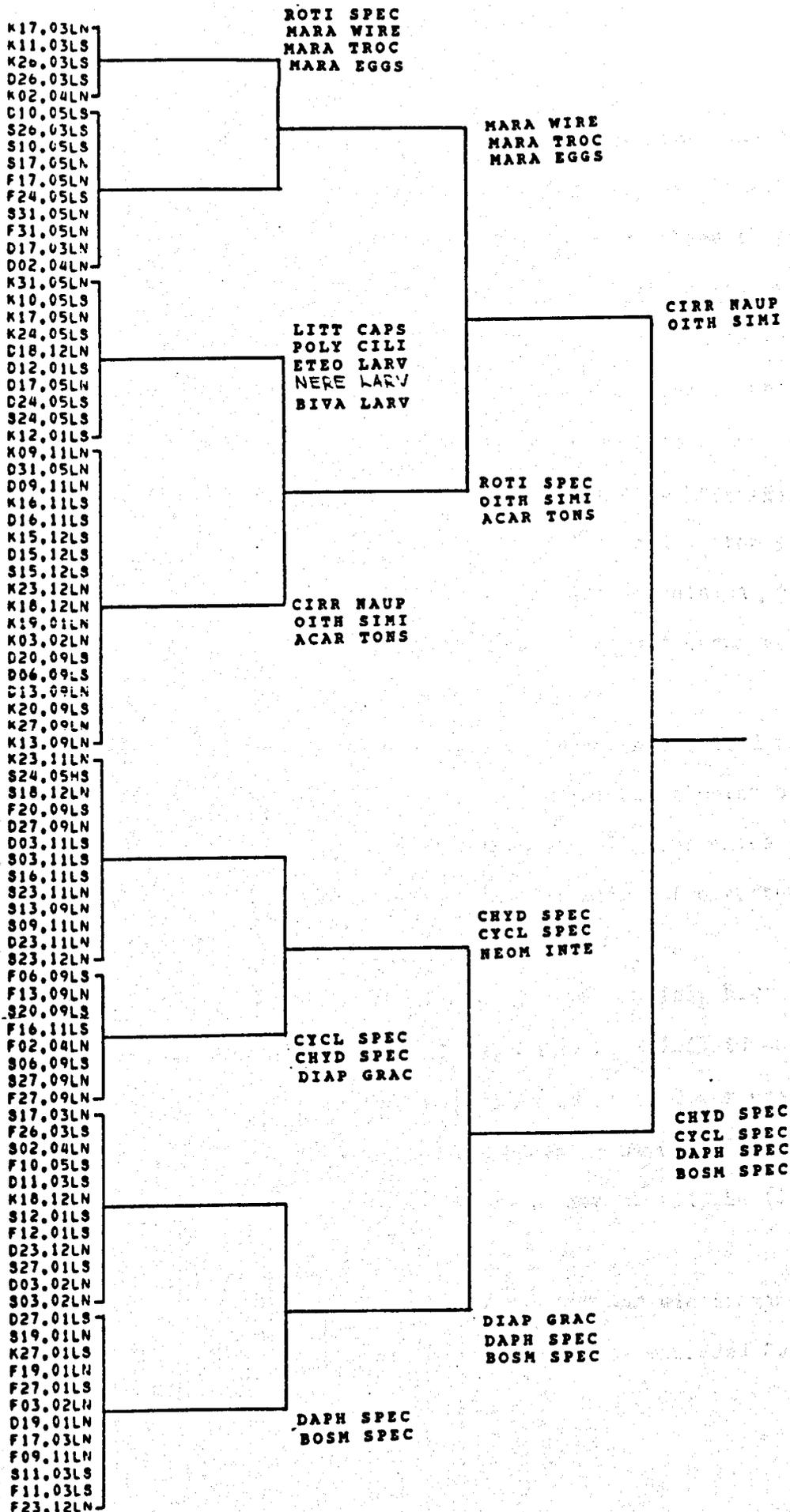


Figure 1.38 Dendrogram of low tide samples classified by Twinspan. Indicator species for each division shown.

Spring tide

The major division was characterised by Pseudocalanus, cirripede nauplii, Oithona, Temora and Polydora on one side and freshwater taxa on the other (Table 1.28). TS and MDA analyses were carried out to level three (Eight groups). Group 1 was most clearly defined by the presence of Centropages, but contained a large variety of neritic copepods and meroplanktonic larvae. Littorinid eggs and veligers were most faithful to groups 1 and 3, while group 2 contained a cluster of A.tonsa occurrences but no terebellid larvae and few Centropages (Table 1.28). Group 3 was defined by a cluster of Maranzelleria occurrences and the absence of A.tonsa. Group 4 differed little from group 3. Group 5 contained, as did group 1, a cluster of samples containing Nereis larvae, but, with the exception of Polydora, lacked frequent occurrences of other larvae and contained virtually no neritic copepods.

Group 6 was defined by another cluster of Maranzelleria, associated with Littorina egg capsules. Group 7 was characterised by another cluster of samples containing A.tonsa, together with the majority of occurrences of Neomysis, while group 8 was identified by the concentration of occurrences of Daphnia, Bosmina, Diaptomus and chydorids.

The dendrogram (Fig.1.39) indicates that groups 1-4 were mainly high tide samples, and almost exclusively from Kincardine, Dunmore, Skinflats and Culross. Group 1 was defined by date (May 1982), while group 2 was predominantly composed of samples collected in September and November-January. The association of these temporal groups is a feature common to all the tidal categories considered thus far.

Group 5 consisted of a mixture of predominantly autumn and winter samples, included representatives of all upper-estuary stations but excluded Culross

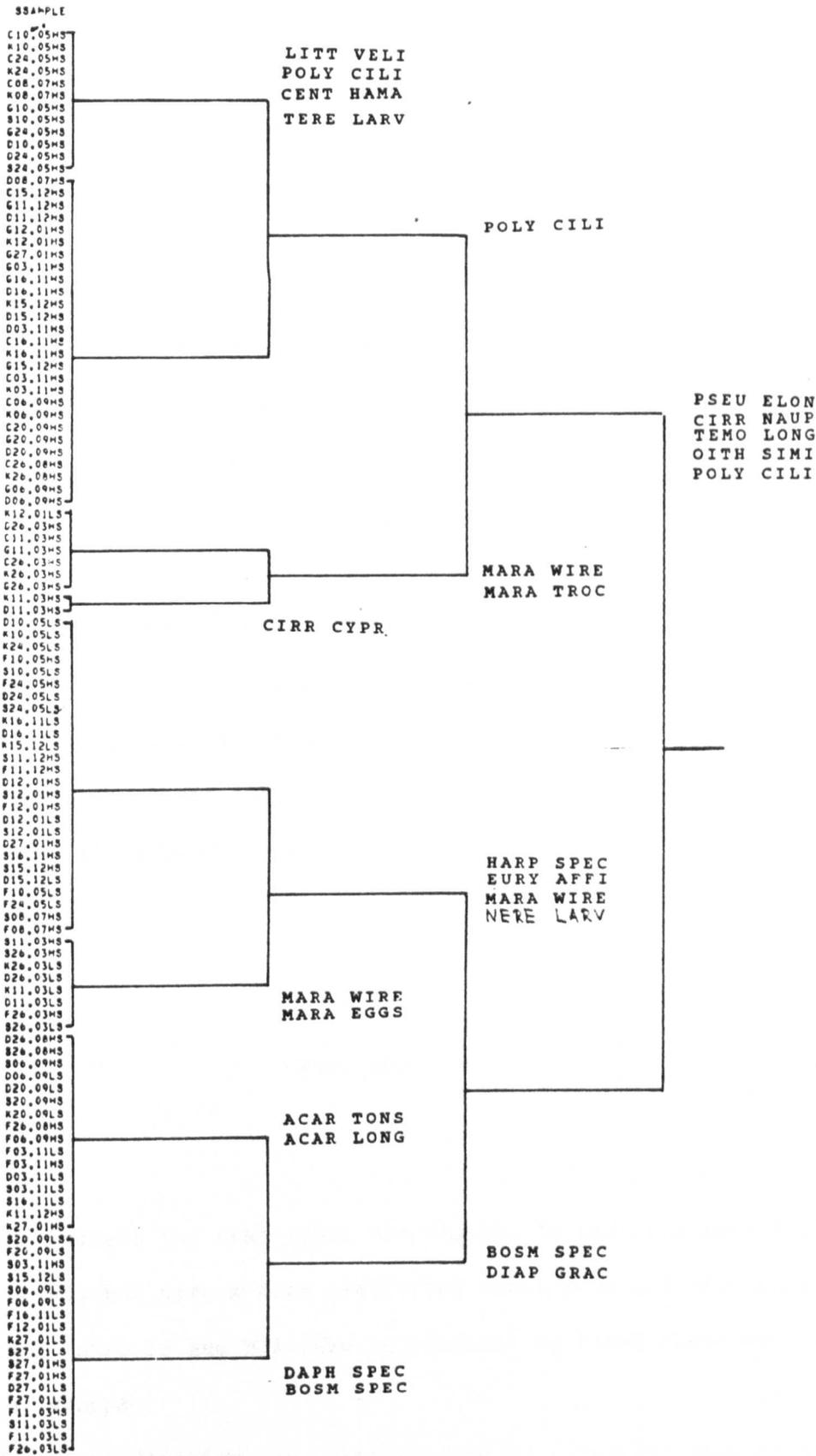


Figure 1.39 Dendrogram of Spring tide samples classified by Twinspan. Indicator species for each division shown.

and Skinflats. Group 6 is confined to March 1982 and mainly low tides. Group 7 is a mixture of predominantly autumn and winter samples, mainly low tide and with a bias towards the upper estuary stations, and group 8 continues this trend with an increased representation of Fallin and S.Alloa samples.

The MDA plot (Fig.1.42a) reflects the above observations clearly; the noted similarity between groups 1 and 2, and also between 3 and 4, is well-defined. The vectors correctly indicate that these two pairs should differ most in respect of AR, Chla, Temp and Date, but little in respect of Sal.

Dist, %org and Sal are clearly aligned, are virtually orthogonal to Date and Disch (which are opposite to each other), and act in the opposite direction to Inor and Phaeo. Chla is aligned with Date, and helps to distinguish groups 5 and 7 from 3,4 and 6. Groups 3,4 and 6 are in fact all samples taken in March 1982.

Neap tide

The pattern for neap tides was similar to that for spring tides (Table 1.29, Fig.1.40) but with a more restricted occurrence and abundance of most larval taxa. TS and MDA were carried out to level three division, producing eight groups.

The major division was characterised by cirripede nauplii on one side and

and Neomysis, Diaptomus, Bosmina, Daphnia on the other.

At level three, groups 1 and 2 contained most occurrences of polychaete larvae. Centropages was confined to group 2. Groups 3 and 4 contained few larvae other than Polydora and Maranzelleria, but Pseudocalanus, Temora, Oithona and cirripede nauplii were moderately well-represented. The highest Eurytemora and rotifer abundances occurred in group 4. Groups 5 and 6 were distinguished by Daphnia, Bosmina and Diaptomus, with some occurrences of Neomysis. Few taxa were present in samples in groups 7 and 8; Neomysis was the species most diagnostic of group 7.

The pattern of sample clustering by attribute was similar to that noted already for other categories; groups 1-4 tended to be associated with seaward stations, groups 5-8 with landward stations, with a similar trend for tidal state. Sorting by date was most marked in groups 1-4.

MDA illustrated the contrast between spring and neap tides (Fig.1.42b). The relative magnitude and direction of influence of variables was similar (although Date and Disch were antagonistic on spring tides and similar on neap tides), but neap tide group centroids were less widely dispersed; 5,6 and 7 especially differed little in location. Disch was the variable which best distinguished 8 from 5,6, and 7, and accounts for the concentration of freshwater taxa in the latter.

On neap tides, the importance of distance relative to salinity increases. Xorg was still aligned with these two variables, but Temp was also more aligned with them than on spring tides. Date and Disch were, as in previous categories, almost orthogonal to the major spatial variables. Groups 1 and 3 differ from 2 and 4 in these respects, and this separation seems to relate to Oithona in the former pair (autumn/winter) and high abundance of Eurytemora and Rotifera in the latter (winter to spring).

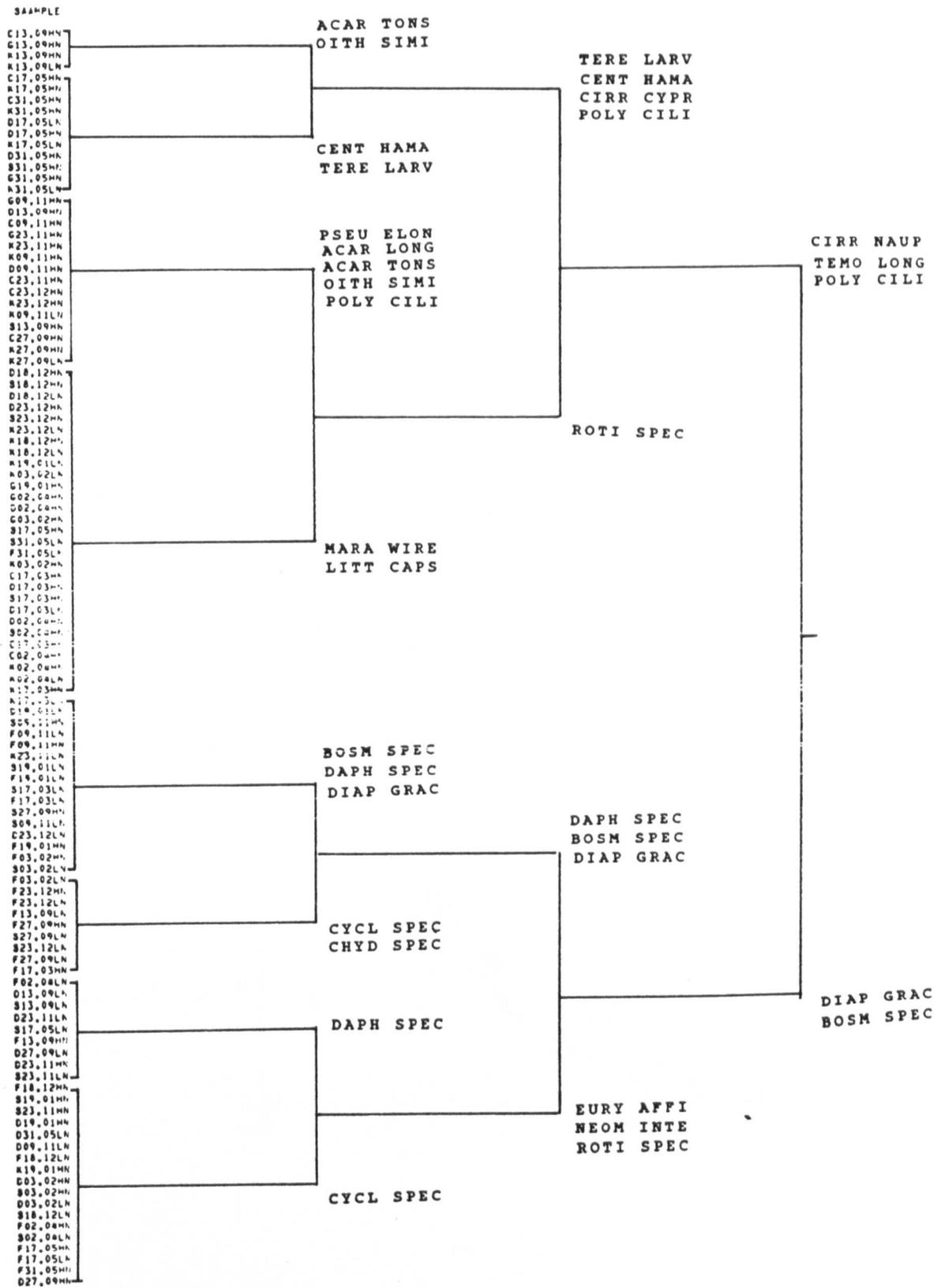


Figure 1.40

Dendrogram of Neap tide samples classified by Twinspan. Indicator species for each division shown.

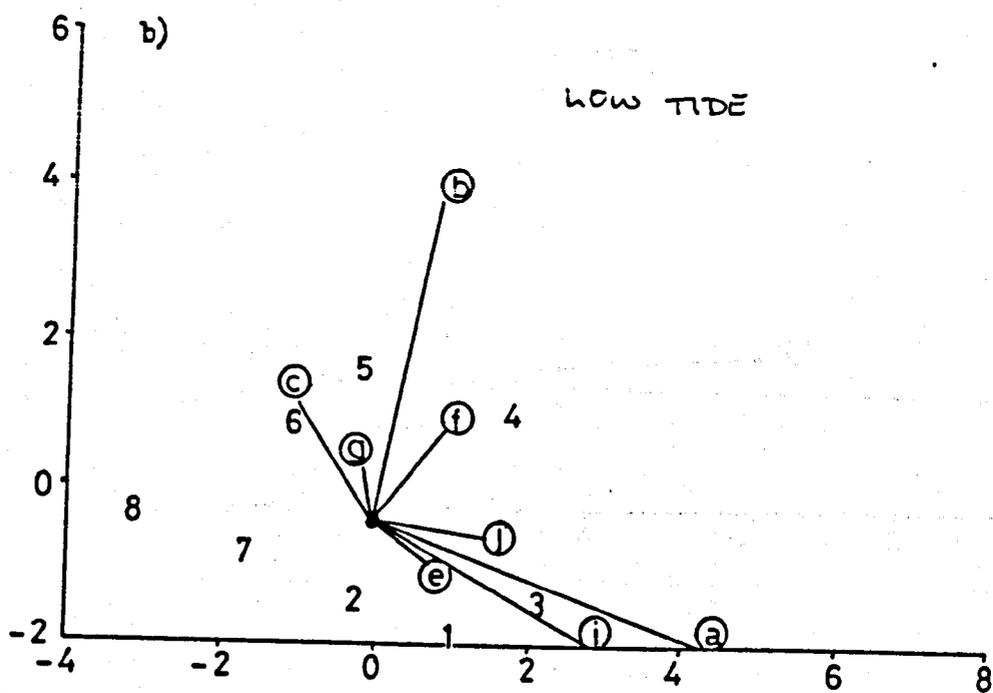
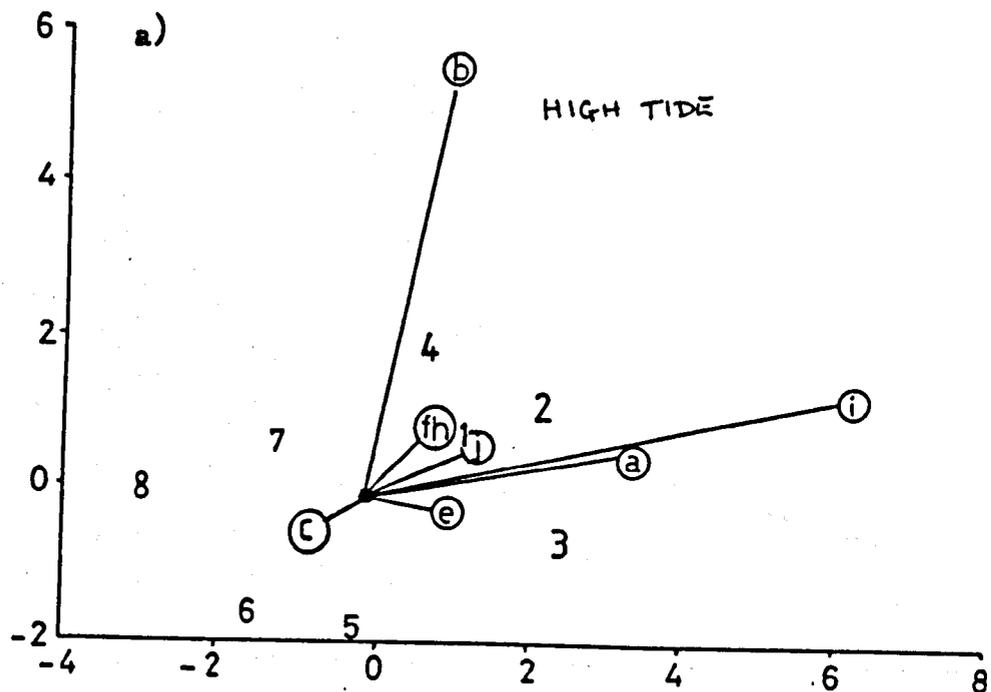


Figure 1.41

Vector plots for a) high tide samples and b) low tide samples showing the location of the centroids of 8 Twinspan groups ordinated in Discriminant space on the basis of sample 'environmental' attributes. Vectors indicate positive direction and relative magnitude of influence of variables in discriminating between groups. Vector labels indicated in text.

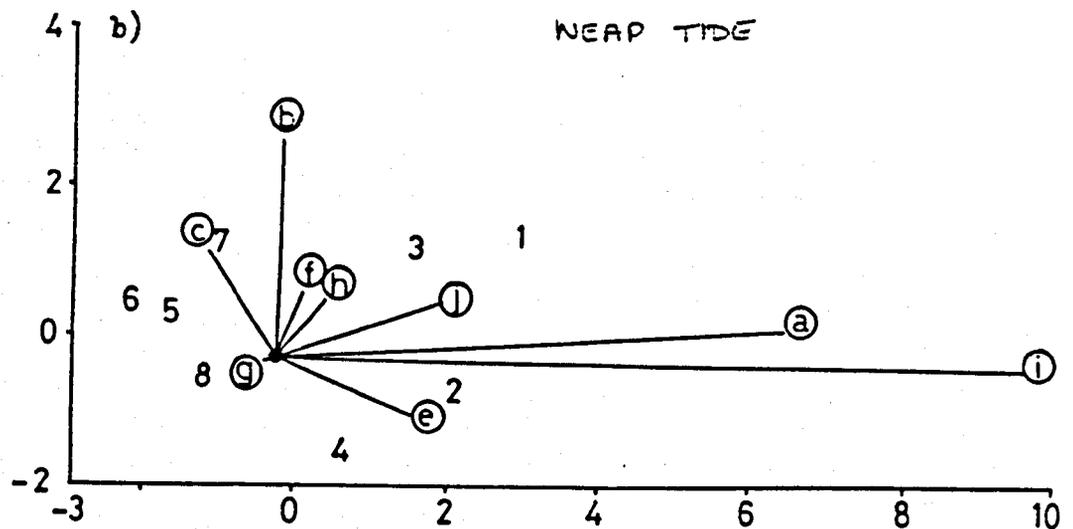
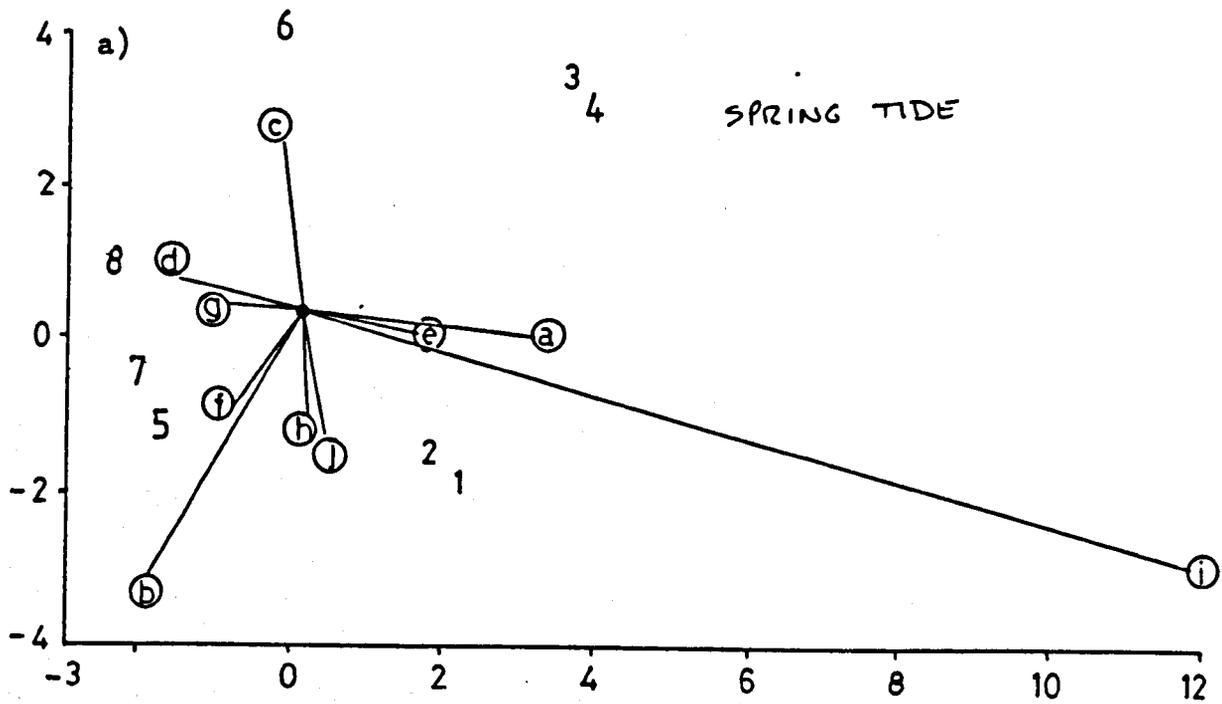


Figure 1.42

Vector plots for a) spring tide samples and b) neap tide samples showing the location of the centroids of 8 Twinspan groups ordinated in Discriminant space on the basis of sample 'environmental' attributes. Vectors indicate positive direction and relative magnitude of influence of variables in discriminating between groups. Vector labels indicated in text.

Chapter 2

Measurements of development rate in E. affinis

Experiments were carried out in June and July 1983 and March-May 1984 to measure the development rates of E.affinis in estuary water at a range of temperatures representative of conditions in the Forth estuary(8 deg.C-20 deg.C, Figs.1.3-1.5). Attempts were made to maintain lighting, salinity and food at approximately natural levels.

Experiment 1 : Development rates in mass culture

A preliminary study was conducted in June-July 1983 to establish the feasibility of culturing E.affinis in estuary water on natural suspended particulate material. A variety of methods have been described for following the development of copepods through successive instars; these range from the regular sacrifice of replicate cultures (Heinle 1966) to the repeated subsampling of a continuous culture (Vidal, 1980a). The latter method was adopted in the first instance in this study as offering the expectation of a more exact relationship between successive samples.

Egg-sac-bearing female E.affinis were obtained by hand-net at S.Alloa(Fig.1.2) Animals collected in the net were washed gently into the cod-end and decanted into a 1 litre container half-filled with habitat water. Salinity and temperature during sampling were continuously monitored using an MC5 temperature-salinity bridge. A 25 l water sample was collected when the salinity was between 14‰ and 16‰. Temperature was between 15 deg.C and 17.5 deg.C during sampling.

The copepod container was placed in a cool-box, and transferred to the laboratory within 1 hour of collection. Animals were sorted immediately on arrival, in a CT room at 15 deg.C, using a Perspex sorting device (Nival and Nival 1970). Copepods were drawn into the observation chamber by siphon from a reservoir; the chamber acted as a tap by means of which individuals could be directed either to a collecting vessel or to waste. 200 egg-sac-bearing female E.affinis were sorted in this manner without sustaining visible damage.

A 1 litre sample of habitat water was filtered onto a pre-ashed, tared, Whatman GF/C filter. The filter was rinsed 3 times with 10 ml distilled water, dried at 60 deg.C for 24h and weighed after cooling in a dessicator. Following this, the filter was ashed for 6h at 450 deg.C and re-weighed. A blank filter (filtered seawater only) was subjected to the same treatment. Dry and ash weights were corrected for blank values, and ash-free dry weight calculated as mg/l.

The remaining 24 litres of water sample was screened through 69 um nylon mesh to remove microzooplankton, and held in dim light at 15 deg.C until required.

Vidal (1980) followed development of Calanus and Pseudocalanus in 10 l vessels from which 10% of the population was subsampled at varying intervals. In the present experiment, 2 litre vessels were established at 15 deg.C and 20 deg.C, using well-mixed habitat water (15 +/- 1 %) screened and held as described above. 15 deg.C water was allowed to acclimate to 20 deg.C for 24h before use. Initial suspended solids were estimated to be 75 mg/l. Suspended solids levels in the culture vessels were not monitored during the experiment.

On 26.6.83, 100 egg-bearing females were added to a vessel at each temperature. The 15 deg.C vessel was maintained in a cooled incubator with the lighting cycle adjusted to contemporary conditions. The 20 deg.C vessel was maintained under ambient lab. conditions and was therefore subject to less control. Both vessels were covered to minimise salinity changes, and were topped up to where necessary to a marked level with distilled water before sampling took place. Vessel contents were not mixed between sampling events, and particulate material eventually settled out on the bottom of the vessels.

Each vessel was sampled at intervals of approximately one and three days, at mid-afternoon. Vessel contents were well-mixed, and 5% of the volume sampled by rapidly immersing and filling a 100ml beaker. The contents of the beaker were preserved by the addition of Steedman's solution to a final concentration of 4% and were subsequently concentrated to a volume of 5 ml by decanting through a 100 ml polystyrene vessel with 69 um mesh-covered holes near the base. The sample was then counted, and specimens identified to developmental stage. The descriptions of instar characteristics given by Katona (1971) were followed carefully, to minimise the possibility of including instars of other species which may have been included as eggs in the initial inoculum.

Following sampling, the 24 l reservoir was thoroughly agitated and a 100 ml sample withdrawn and added as replacement to each culture vessel.

The experiment was terminated in each vessel when either a cohort appeared to have reached adulthood, or no remaining animals could be detected.

Experiment 2 : development rates at four temperatures
and two food levels

Between 26.3.84 and 21.5.84, development rate in E.affinis was investigated in greater detail and under more carefully controlled and realistic conditions.

Throughout this series of tests, regular collections of habitat water were made in order to maintain a degree of coupling between the laboratory and estuarine systems.

Development rate was measured at four temperatures (8,12,16 and 20 deg.C) and at two food levels (10 and 50 mg/l natural suspended particulate material). The range of temperatures spanned, within practical limits, the greater part of the range experiences annually in the Forth. Temperatures of 5,10,15 and 20 deg.C would have been preferable (as spanning a wider range and permitting a more direct comparison with the literature), but it was not feasible to achieve a temperature lower than 8 deg.C with the available facilities.

The food levels were chosen to reflect the range typical of Forth near-shore waters under calm, slackwater conditions (see results of field survey). Neither food level was expected to be limiting in terms of available energy and nutrients; measurements in 1982 indicated that the organic content of suspended particulate material never fell below 9.7% and was commonly 20-25%. If half of the organic content is assumed to be carbon, then a minimum of approximately 500 ug/l would have been available initially in any treatment. This matches the highest feeding level used by, for instance, Klein Breteler et al (1982) in their study of the growth and development of four species of North Sea calanoids. The nutritional quality of the suspended particulate material was not known, but field observations had shown previously that the estuary could

support locally substantial populations during periods of low primary productivity. At each temperature, cultures were replicated four times at the higher food level and twice at the lower food level.

Adult female E.affinis with eggs in their body cavities and bearing spermatophores were obtained and sorted as described above, from S. Alloa on 23.3.84. A further sample of males and females were held as stock for re-mating. Salinity was 12.6 ‰ and the temperature 8.5 deg.C.

Females were placed individually in 5 ml of habitat water in tissue culture plates, held in a cooled incubator at 8 deg.C, and observed daily until egg sacs were produced. When sufficient eggs had been produced to initiate a test at one temperature, the egg-bearing females were transferred to 20 ml vessels in an incubator or C.T. room at the appropriate experimental temperature and the vessels allowed to equilibrate. These vessels were examined daily at 1000 h and all nauplii present collected with a Pasteur pipette with a tip drawn out to a diameter of approximately 100 μ m. 600 nauplii of less than 24h age were used per experimental temperature.

Each of the six vessels used to investigate naupliar development at each temperature consisted of a 120 ml polystyrene jar with 2 1cm holes cut diametrically opposite each other 5 mm from the base. The holes were covered with 69 μ m mesh nylon net, and permitted the vessels to be gently drained and the nauplii concentrated into a small volume of water. This facilitated observation, sampling, and the changing of water.

When development to the first copepodite stage had been completed, animals were transferred to 69 μ m mesh net cylinders of approximately 500 ml volume.

These cylinders were equipped with a clear polystyrene base (90 mm Petri dish) into which the copepodites could be concentrated. The cylinders were stiffened with glass rods to enable them to stand upright in the culture medium.

The development vessels were placed in polythene baths of 10l capacity, which were filled to a depth of 1 cm less than the vessels' height with with 69- μ m screened habitat water. This water had been adjusted with 1.2 μ m filtered river water (0 %) to a salinity of 15 ‰. Further adjustments were made with either a filtered volume of this 15 ‰ mixture or with resuspended filter contents to produce a nominal suspended particulate concentration of 10 or 50 mg/l. Suspended solids determinations were carried out on the source water as described previously, but the accuracy of the suspended solids adjustment was not routinely verified.

As the vessels were placed in the tanks, they rapidly filled with water and suspended particles. To maintain the particulate material in suspension and ensure circulation through the vessels, each tank was equipped with a small centrifugal pump (Eheim aquarium pump, 4l/min. flow rate). The pump abstracted water from one end of the tank, and returned it via a simple manifold to the other end. Preliminary testing with Rose Bengal dye introduced via a Pasteur pipette indicated that this was sufficient to generate gentle water flow through the development vessels and to ensure even temperature distribution.

Expanded polystyrene sheets were arranged over the vessels, and these diffused and attenuated the overhead lighting (natural light/dark cycle) to approximately 1.2 Lux (Leakey, 1983).

The water in the baths was replaced every 48h, from stock water collected weekly at high tide at S.Alloa and Stirling. This water was adjusted to approximately experimental salinity and particulate content, and stored at the appropriate temperature. Stock water was mixed vigorously twice per day. Chlorophyll a concentrations were measured for each batch of stock water to establish if any increase in primary production had occurred between successive collections.

Tests were initiated by the addition of 100 nauplii to each of the 6 vessels at a given temperature. Two of the 50 mg/l replicates at each temperature were subjected to detailed monitoring. This took place at 2-day intervals at 8 deg.C, one-day intervals at 12 and 16 deg.C, and 12h intervals at 20 deg.C. Test vessels were gently removed from their tanks, concentrating the animals within into a small volume of water. In the copepodite development vessels, a wash bottle filled with tank water was used to gently rinse animals down the mesh into the base dish. Animals were aspirated gently into a Pasteur pipette with a 90 degree bend 2 cm from the tip. The pipette was connected by a length of silicone rubber tubing to a rubber bulb which could be compressed by a screw clamp (Boleyn 1967). The Pasteur pipette tip was placed flat on the base of a Petri dish containing tank water, and the animals expressed slowly, one or two at a time, into the dish.

Copepods in the last 2 cm of the pipette were observed at 100x magnification and their developmental stage recorded with the aid of a bank of tally counters labelled for each stage. A minimum of 50 individuals were staged on each occasion.

The two remaining high-food replicates, and the two low-food replicates, were maintained as controls for handling effects on development rate and mortality.

These vessels were only drained gently and checked at low power for the first appearance of copepodite stages 1 and 6.

The test continued at each temperature until all specimens in a sample were adult. C.T. room temperature and tank water temperature were recorded daily.

Egg development rates were estimated separately. Thirty mated females were held individually in 2ml tissue culture well plates, and observed at 12 h (16 and 20 deg.C) or 24h (8 deg.C) intervals. The approximate times of egg sac production and naupliar hatching were recorded.

Results

Preliminary experiment: development rates in mass culture at 15 and 20 deg.C

The preliminary experiment was of limited success. The 20 deg.C culture collapsed after 14 days, following the first appearance of c4 copepodites. Naupliar development rates appeared relatively constant between instars; the first c1 individuals appeared after 5 days. Subsequently, development proceeded to c3 in a further 4 days before stagnating during the remaining 6 days.

Development was more complete at 15 deg.C (Fig.2.1). The culture was terminated after 30 days, following the first appearance of adults of both sexes on day 27. A small number of adult females were recorded on days 20 and 23; earlier appearances of adult females were attributed to the initial inoculum. Individuals were widely distributed amongst stages on most days. The first copepodites were present in samples between 6 and 9 days, with c3 copepodites appearing on the 12th day. Total copepodite development time thus appeared to be approximately twice total naupliar development time.

The persistence of early developmental stages throughout the experiment may indicate that a male or males were inadvertently included in the initial inoculum, and that some of the females were subsequently re-mated.

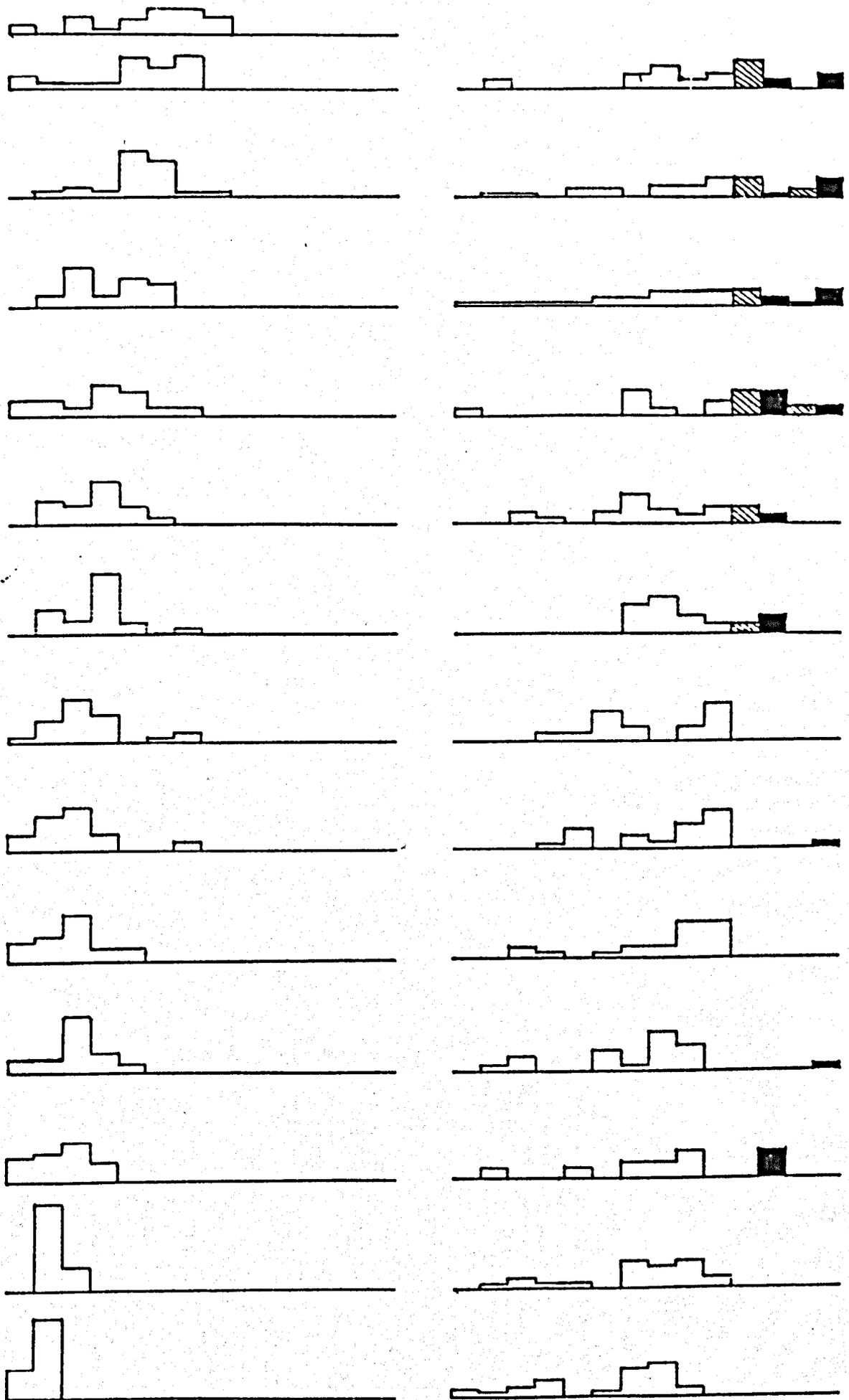


Figure 2.1 Development of *E. affinis* at 15 deg.C in mass culture:
 Stage distribution in successive samples (left to right,
 top to bottom). Male and female c5 and c6 shaded (males hatched, females black).

Experiment 2 : Development of cohorts at two food levels and four temperatures

Primary production

Chlorophyll a concentrations in sample water did not exceed 4.7 ug/l during the experiment.

Comparison of development and survival between replicates and food levels

The date of first appearance of c1 and c6 stages was recorded for each of the 6 vessels at each of 4 temperatures (Table 2.1). The comparisons of most interest are a) between high-food replicates subjected to detailed monitoring and those followed with minimal disturbance and b) between either high-food category and the low-food replicates. A full comparison was not possible for b) at 16 and 20 deg.C as the appearance of c1 individuals was missed. It is nevertheless apparent that neither handling nor food level had any discernible systematic effect on development rates; specifically, repeated handling or lower food availability did not impede development with respect to animals subjected to minimal handling or fed ad lib.

Overall, survival ranged from 59% (16 deg.C, high food) to 86% (12 deg.C, high food)(Table 2.2). Females constituted between 45% and 58% of the final population. There was no trend in survivorship between high and low-food treatments or between temperatures.

Table 2.1 Day of first appearance of copepodite 1 and copepodite 6 stages at 4 temperatures and two food levels. earliest day for combined replicate counts underlined.

TEMPERATURE (°C)	FOOD LEVEL (mg/l)			
	50		10	
	c1	c6	c1	c6
8	15	33	17	35
	17	33	17	35
	<u>15</u>	<u>35</u>		
12	9	21	9	23
	10	22	10	23
	<u>8</u>	<u>22</u>		
16	5	14	-	14
	6	15	-	15
	<u>6</u>	<u>14</u>		
20	5.5	13.0	-	13.0
	5.5	13.5	-	14.0
	<u>4.5</u>	<u>14.0</u>		

Table 2.2 Percent survival and percent adult female in replicate trials conducted at four temperatures and two food levels

Food level		Percent survival (% female in brackets)			
		8	12	16	20
High	1	76(52)	86(58)	73(54)	80(49)
	2	74(48)	64(50)	63(56)	68(53)
	3	60(51)	71(47)	83(53)	67(46)
	4	76(55)	65(53)	59(48)	64(52)
Low	1	66(49)	77(47)	71(52)	72(57)
	2	79(45)	69(49)	75(55)	66(50)

In the light of the above observations it was considered justifiable to proceed to estimate stage durations from the combined counts of the two more intensively-monitored high-food replicates at each temperature.

Estimation of egg development times

Successful development of eggs occurred only at three temperatures (Table 2.3); 8, 16 and 20 deg.C. Mean development time ranged from 4.7d at 8 deg.C to 0.5d at 20 deg.C. Development time at 16 deg.C was much closer to that at 8 deg.C than at 20 deg.C.

Table 2.3 Mean egg development times at 3 temperatures

	Temperature			
	8	12	16	20
Mean (Days)	4.7	-	4.0	0.5
Range	(3.5-6.0)	-	(0)	(0)

Estimation of naupliar and copepodite development rates

The process of cohort development through instars can be considered to fall into the category of time-percent solutions derived in toxicological studies. In such studies, cumulative percent reaction versus time follows a characteristically S-shaped curve. Figure 2.3 emphasises the applicability of this approach to development studies. The passage of individuals through each instar is spread over time, with a few entering the next stage at first, followed by the majority at an approximately constant rate, and with a small number completing development after a longer time interval.

Stage duration in the work reported here will be defined as the interval between the median time at which animals enter a stage and the median time at which they enter the next stage. To estimate median development time (DT50), the cumulative percent having moulted beyond a particular stage was plotted against time on log-probability paper and a straight line fitted to the points following Litchfield(1948). The DT50 was estimated graphically from this line.

Development at 8 deg. C

Development to c6 was complete after 45 days (Tables 2.5a-c, Fig.2.2), at which time percent survival ranged from 60 to 79%. Females constituted between 45% and 55% of the survivors.

Naupliar stages appeared generally equal in duration, with the exception of a protracted n2 stage. The distribution of individuals in stages broadened,

Table 2.5a Distribution in stage on each sampling occasion at 8 deg.C;
high-food replicate 1

8°C High food level, replicate 1

	n1	n2	n3	n4	n5	n6	c1	c2	c3	c4	c5	c6
1	50	0										
3	4	46										
5	0	50										
7		50	0	0								
9		35	14	0	0							
11		6	37	6	5							
13		0	2	40	8	0						
15			0	4	39	6	0					
17				0	8	39	3	0				
19					0	16	25	9				
21						0	43	7	0			
23							23	25	2			
25							12	36	2			
27							5	20	25	0		
29							0	6	43	1		
31								0	16	34	0	
33									0	40	10	0
35										34	16	3
37										0	42	8
39											30	20
41											3	47
43											0	50

Table 2.5b Distribution in stage on each sampling occasion at 8 deg.C;
high-food replicate 2

8°C High food level, replicate 2

	n1	n2	n3	n4	n5	n6	c1	c2	c3	c4	c5	c6
1	50	0										
3	9	41										
5	0	50										
7		50	0	0								
9		27	17	7	0							
11		0	44	2	0							
13			8	33	9							
15			0	0	50	0	0					
17					2	43	5					
19					0	17	33	0				
21						0	38	12	0			
23							27	18	5			
25							9	31	10			
27							0	27	23	0		
29								0	44	6		
31									24	26	0	
33									0	44	6	0
35										27	14	9
37										3	38	9
39										0	42	8
41											13	37
43											8	42
45											0	50

Table 2.5c Distribution in stage on each sampling occasion at 8 deg.C;
percentage values from combined replicate counts

8°C High food level, combined counts (percentages)

	n1	n2	n3	n4	n5	n6	c1	c2	c3	c4	c5	c6
1	100	0										
3	14	86										
5	0	100										
7		100	0	0								
9		62	30	8	0							
11		6	82	8	4							
13		0	10	74	16	0						
15			0	4	90	6	0					
17				0	10	82	8	0				
19					0	32	58	10				
21						0	80	20	0			
23							50	44	6			
25							22	66	12			
27							4	48	48	0		
29							0	6	88	6		
31								0	40	60	0	
33									0	84	16	0
35										61	26	12
37										2	80	18
39										0	72	28
41											18	82
43											8	92
45												100

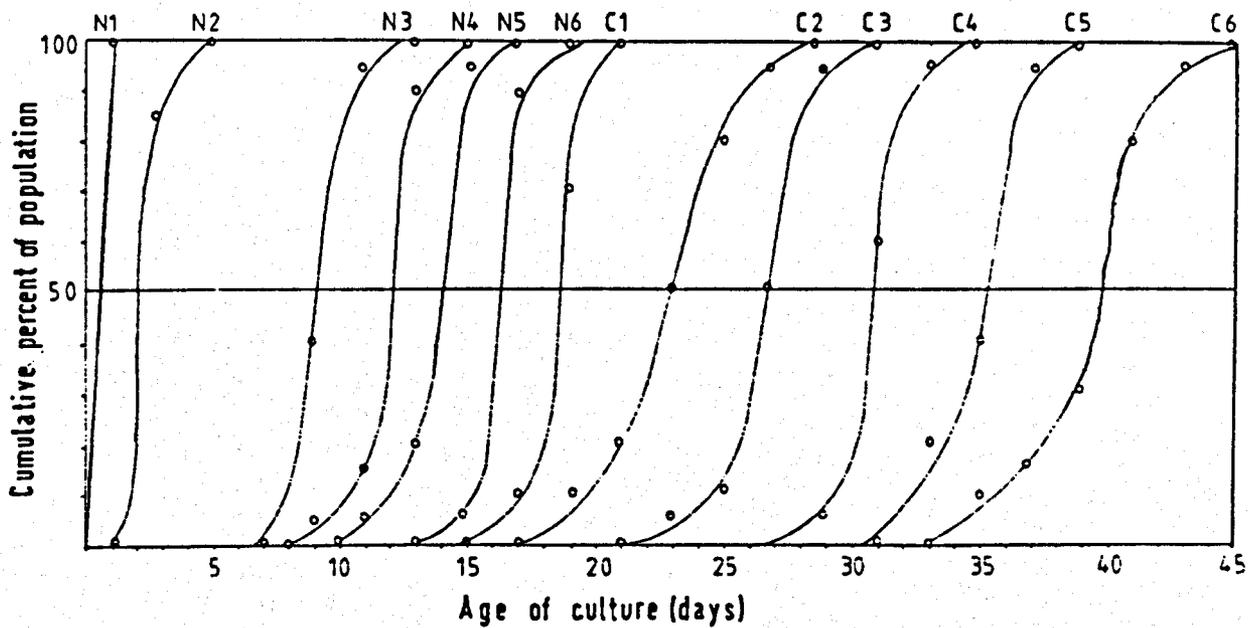


Figure 2.3 Cumulative percent of population beyond a given stage on each sampling date at 8 deg.C, high food level. Curves fitted by eye

and stage duration increased, in the later copepodite stages.

Naupliar stage durations, derived from the DT50 values (Table 2.4), were, with the exception noted above, of about 2.5 days. The n2 stage lasted considerably longer at 6.75 days.

Development to c1 was estimated to take 18.20 days (Table 2.4), while full development (50% moulted to c6) was estimated at slightly more than twice this at 39.0 days.

Development at 12 deg.C

All surviving copepods had reached adulthood after 29 days. As at 8 deg.C, the distribution of individuals in stages broadened with increasing age (Fig.2.4), but the development curves were considerably straighter than at 8 deg. and the stage intervals less variable. Total median development time for all naupliar stages was 10.40 days, and full development was estimated to take 26.0 days (Table 2.4). The n2 stage was again slightly longer at 2.55 days than the other naupliar stages, which ranged from 1.20 to 1.80 days.

Copepodite development took longer than naupliar development (15.6 days versus 10.4 days). Individual stage durations ranged from 3.00 to 3.50 days.

With the exception noted above (n2 stage), there was no systematic variation in naupliar instar duration or in copepodite instar duration.

Table 2.4 Stage duration and median stage development time at four temperature, high-food treatment

Stage	8°C		12°C	
	Duration	DT ₅₀	Duration	DT ₅₀
N1	2.45	0	1.70	0
N2	6.75	2.45	2.55	1.70
N3	1.95	9.20	1.85	4.25
N4	2.10	11.15	1.30	6.10
N5	2.55	13.25	1.20	7.40
N6	2.40	15.80	1.80	8.60
C1	4.05	18.20	3.10	10.40
C2	4.25	22.50	3.25	13.50
C3	4.00	26.50	3.50	16.75
C4	4.00	30.50	2.75	20.25
C5	4.50	34.50	3.00	23.00
C6	--	39.00	--	26.00

Stage	16°C		20°C	
	Duration	DT ₅₀	Duration	DT ₅₀
N1	1.40	0	0.95	0
N2	1.90	1.40	1.40	0.95
N3	0.95	3.30	1.10	2.35
N4	0.75	4.25	1.05	3.45
N5	0.95	5.00	1.05	4.50
N6	1.10	5.95	1.45	5.55
C1	1.35	7.05	1.55	7.00
C2	2.10	8.40	1.95	8.55
C3	1.90	10.50	1.75	10.50
C4	2.10	12.40	1.65	12.25
C5	2.50	14.50	1.35	13.90
C6	--	17.00	--	13.25

Table 2.6a Distribution in stage on each sampling occasion at 12 deg.C;
high-food replicate 1

	n1	n2	n3	n4	n5	n6	c1	c2	c3	c4	c5	c6
1	50	0										
2	7	43	0									
3	0	43	7									
4		34	16									
5		17	33	0								
6		2	28	20	0							
7		0	14	31	5							
8			0	7	43	0						
9				0	30	20	0					
10					0	36	14	0				
11						31	16	3				
12						10	30	10				
13						0	37	13				
14							28	22				
15							17	33	0			
16							0	45	5			
17								22	38	0		
18								5	39	6		
19								0	44	6		
20									29	21	0	
21									19	28	3	
22									10	31	9	0
23									0	26	23	1
24										12	35	3
25										0	40	10
26											31	19
27											25	25
28											21	29
29											0	50

Table 2.6b Distribution in stage on each sampling occasion at 12 deg.C;
high-food replicate 2

	n1	n2	n3	n4	n5	n6	c1	c2	c3	c4	c5	c6
1	50	0										
2	12	38	0									
3	0	49	1									
4		39	11									
5		24	26	0								
6		6	20	24	0							
7		0	8	36	6	0						
8			0	13	31	6						
9				0	20	30	0					
10					0	41	9					
11						29	21	0				
12						13	35	2				
13						0	34	16				
14							16	34				
15							8	42	0			
16							0	48	2			
17								18	32	0		
18								0	40	10		
19									38	12		
20									23	27	0	
21									9	32	9	
22									0	33	17	0
23										8	37	5
24										3	30	17
25										0	31	19
26											24	26
27											9	41
28											0	50

Table 2.6c Distribution in stage on each sampling occasion at 12 deg.C;
percentage values from combined replicate counts

	n1	n2	n3	n4	n5	n6	c1	c2	c3	c4	c5	c6
1	100	0										
2	19	81	0									
3	0	92	8									
4		73	27									
5		41	59	0								
6		8	48	44	0							
7		0	22	67	11	0						
8			0	20	74	6						
9				0	50	50	0					
10					0	77	23	0				
11						60	37	3				
12						23	65	12				
13						0	71	29				
14							44	56				
15							25	75	0			
16							0	93	7			
17								40	60	0		
18								5	79	16		
19								0	82	18		
20									52	48	0	
21									28	60	12	
22									10	63	27	0
23									0	34	60	6
24										15	65	20
25										0	71	29
26											55	45
27											34	66
28											21	79
29											0	100

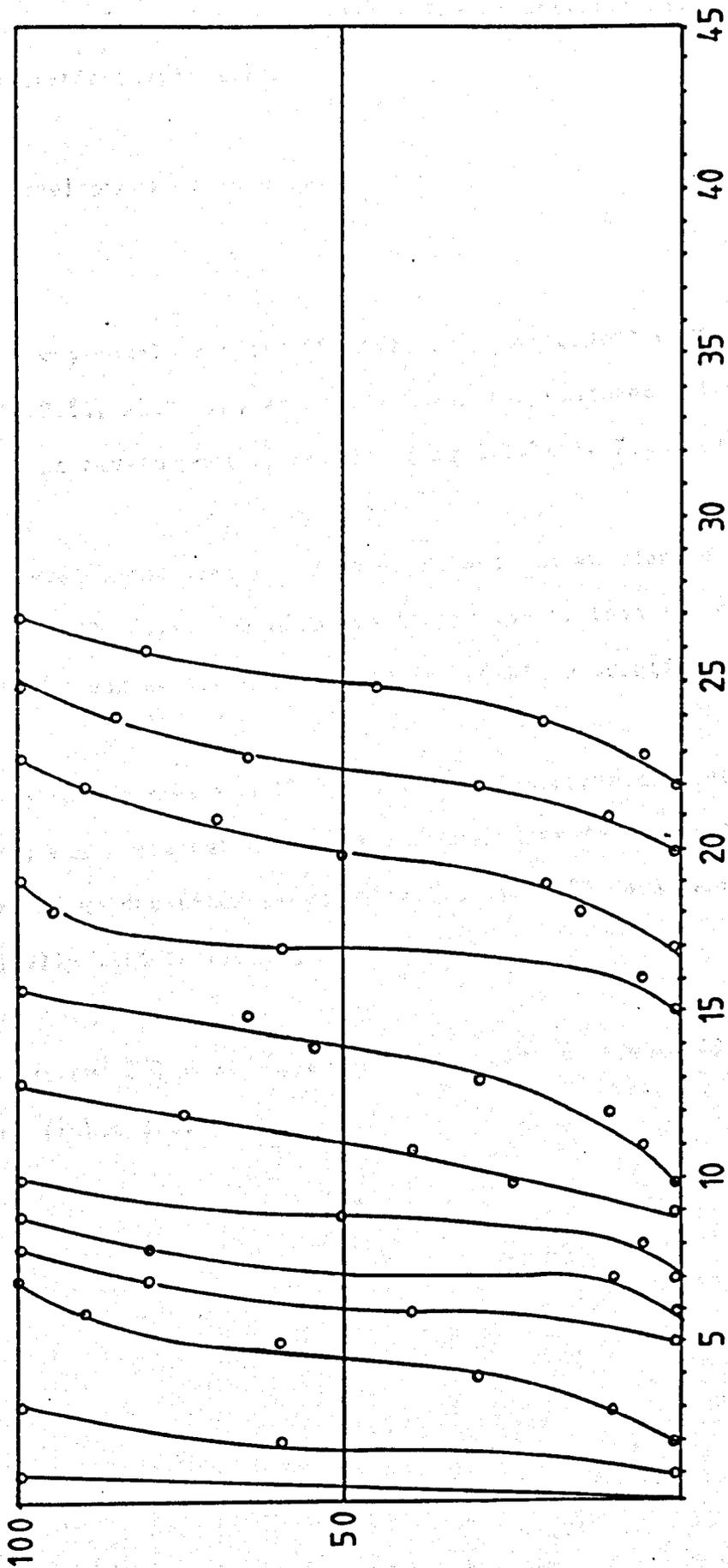


Figure 2.4 Cumulative percent of population beyond a given stage on each sampling date at 12 deg.C, high food level. Curves fitted by eye

Percent survival ranged from 65 to 86, and females constituted between 47% and 58% of the population (Table 2.2).

Development at 16 deg. C

Development to c6 was complete after 20 days. The development curves were almost linear (Fig.2.5), although, as at the lower temperatures, stage duration broadened as development progressed (Fig.2.5, Table 2.10a-c).

Median naupliar development time was 7.05 days, and median stage duration ranged from 0.75 to 1.90 days. The n2 stage lasted longer than any other naupliar stage. There was no trend in the remaining stage duration variation.

Total median development time was 17 days, and median copepodite development time, at 9.95 days was again rather longer than naupliar development time. Median copepodite stage durations ranged from 1.35 to 2.50 days, and did not change systematically with increasing age.

Survival ranged between 59% and 83%, and females numbers between 48% and 56% of the population (Table 2.2)

Table 2.10a Distribution in stage on each sampling occasion at 16 deg.C;
high-food replicate 1

	n1	n2	n3	n4	n5	n6	c1	c2	c3	c4	c5	c6
1	50	0										
2	0	50	0									
3		35	15									
4		15	35	0	0							
5		0	5	16	29	0						
6			0	0	20	30	0					
7					0	11	39					
8						0	50	0				
9							7	43	0			
10							0	35	15	0		
11								12	25	13		
12								0	27	23		
13									11	39	0	
14									0	39	11	0
15										26	23	1
16										15	29	6
17										0	30	20
18											24	26
19											13	37
20											0	50

Table 2.10b Distribution in stage on each sampling occasion at 16 deg.C;
high-food replicate 2

	n1	n2	n3	n4	n5	n6	c1	c2	c3	c4	c5	c6
1	50	0										
2	0	50	0									
3		30	20	0								
4		5	27	18	0							
5		0	0	7	43	0						
6			0	0	11	39	0					
7				0	0	8	42	0				
8					0	0	41	9				
9							4	46	0			
10							0	31	19	0		
11							0	18	25	7		
12								0	20	30	0	
13									18	26	6	0
14									10	22	16	2
15									0	10	32	8
16										0	29	21
17											17	33
18											8	42
19											0	50

Table 2.10c Distribution in stage on each sampling occasion at 16 deg.C;
percentage values from combined replicate counts

	n1	n2	n3	n4	n5	n6	c1	c2	c3	c4	c5	c6
1	100	0										
2	0	100	0									
3		65	35	0								
4		20	62	18	0							
5		0	5	23	72	0						
6			0	0	31	69	0					
7					0	19	81	0				
8						0	90	10				
9							11	89	0			
10							0	66	34	0		
11								30	50	20		
12								0	47	53	0	
13									29	65	6	0
14									10	58	30	2
15									0	36	55	9
16										15	58	27
17										0	47	53
18											32	68
19											13	87
20											0	100

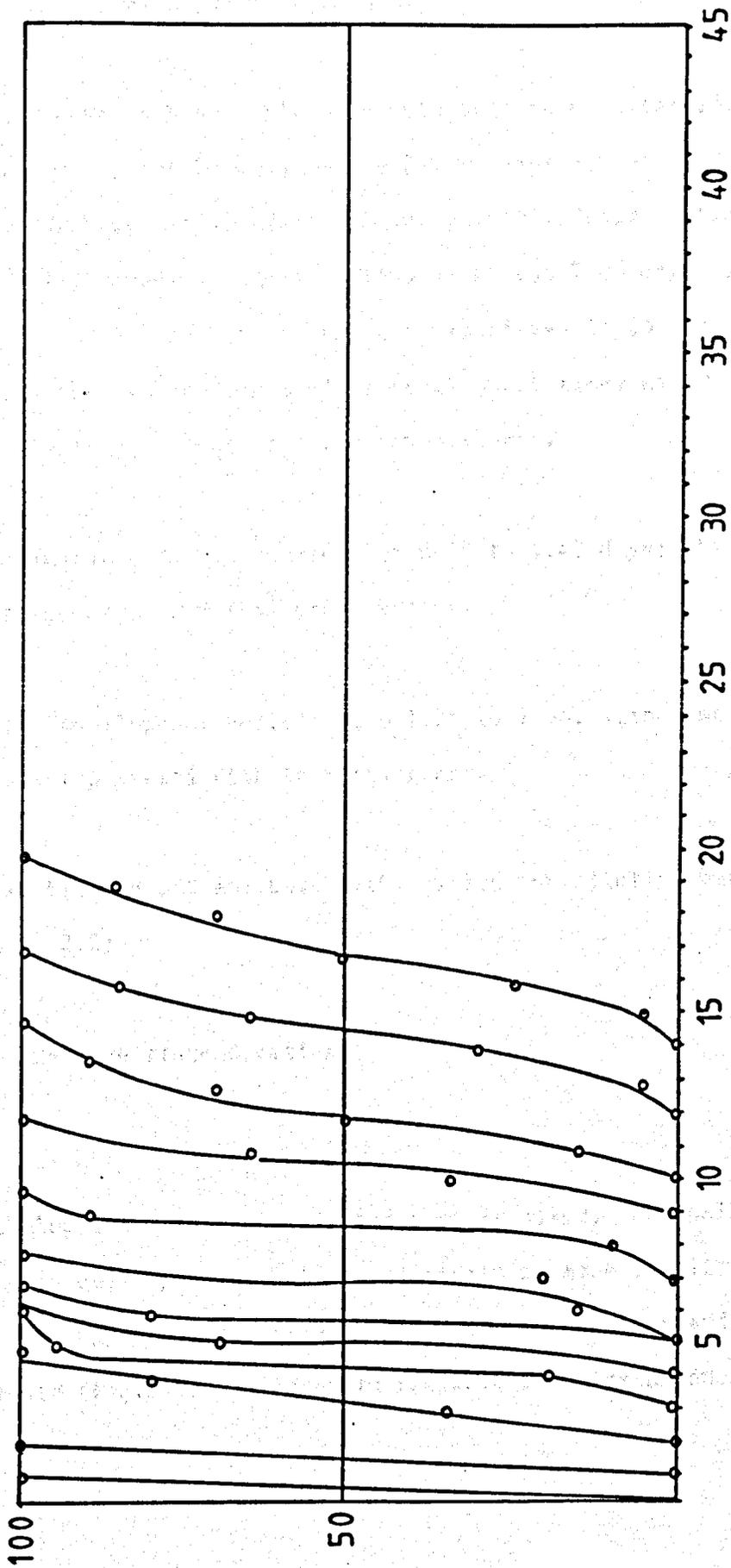


Figure 2.5 Cumulative percent of population beyond a given stage on each sampling date at 16 deg.C, high food level. Curves fitted by eye

Development at 20 deg. C

All surviving specimens had completed development to c6 after 15.5 days. Stage duration was much reduced compared to lower temperatures, and there was less obvious variation in the distribution of individuals within stages (Fig.2.9, Table 2.7). Median development time to n6 was 7.00 days, similar to that at 16 deg. C. The median development time to c6 was 15.25 days. The difference between naupliar and copepodite development times at 20 deg. C was therefore small compared to that at lower temperatures.

Median naupliar instar duration ranged from 0.95 to 1.40 days; the n2 stage again occupied a longer period than other stages.

Median copepodite development periods were 1.35 to 1.95, with some indication of a trend to reducing period with increasing age.

Survivorship was between 64% and 80%, with females constituting between 49% and 57% (Table 2.2).

Average stage duration

When median development times were plotted against stage, the shallower slope of copepodite development at all temperatures is more readily apparent, as is the approximately linear nature of the naupliar and copepodite segments (Fig.2.6). In order to estimate mean instar durations,

Table 2.7 a

20°C High food level, replicate 1

	n1	n2	n3	n4	n5	n6	c1	c2	c3	c4	c5	c6
0.5	50	0										
1.0	30	20	0									
1.5	0	45	5									
2.0		42	8									
2.5		35	15	0								
3.00		27	18	5								
3.5		9	12	20	0							
4.0		0	8	10	2							
4.5			0	30	20	0						
5.0				15	30	5						
5.5				0	22	28	0					
6.0					15	31	4					
6.5					3	37	10	0				
7.0					1	20	28	1				
7.5					0	9	41	0				
8.0						7	26	17				
8.5						0	21	29				
9.0							15	35				
9.5							11	39	0			
10.0							0	28	22	0		
10.5								20	27	3		
11.0								10	28	12		
11.5								0	32	18		
12.0									36	14		
12.5									17	33		
13.0									15	33	0	
13.5									12	28	10	0
14.0									2	13	32	3
14.5									0	6	39	5
15.0										0	23	27
15.5											0	50

Table 2.7b Distribution in stage on each sampling occasion at 20 deg.C;
high-food replicate 2

	n1	n2	n3	n4	n5	n6	c1	c2	c3	c4	c5	c6
0.5	50	0										
1.0	42	8										
1.5	0	50	0									
2.0		47	3									
2.5		36	4	0								
3.0		21	24	5								
3.5		0	17	33	0							
4.0			2	29	19	0						
4.5			0	7	31	12						
5.0				5	33	12						
5.5				0	17	33						
6.0					10	40	0					
6.5					7	40	3					
7.0					3	31	16	0				
7.5					0	14	29	7				
8.0						6	31	13				
8.5						0	28	22				
9.0							26	24				
9.5							9	41	0			
10.0							0	17	33	0		
10.5								11	32	7		
11.0								4	34	12		
11.5								0	40	10		
12.0									36	14		
12.5									18	32	0	
13.0									11	36	3	
13.5									7	27	16	0
14.0									0	3	24	23
14.5										0	11	39
15.0											23	27
15.5											0	50

Table 2.7c Distribution in stage on each sampling occasion at 20 deg percentage values from combined replicate counts

	n1	n2	n3	n4	n5	n6	c1	c2	c3	c4	c5	c6
0.5	100	0										
1.0	72	28	0									
1.5	0	95	5									
2.0		89	11									
2.5		71	29	0								
3.0		48	42	10								
3.5		9	29	62	0							
4.0		0	10	69	21	0						
4.5			0	37	51	12						
5.0				20	63	17						
5.5				0	39	61	0					
6.0					25	71	4					
6.5					10	77	13	0				
7.0					4	51	44	1				
7.5					0	23	70	7				
8.0						13	57	39				
8.5						0	49	51				
9.0							41	59				
9.5							20	80	0			
10.0							0	45	55	0		
10.5								31	59	10		
11.0								14	62	24		
11.5								0	72	28		
12.0									67	33		
12.5									41	59	0	
13.0									26	71	3	
13.5									19	55	26	0
14.0									2	16	56	26
14.5									0	6	50	44
15.0										0	23	77
15.5											0	100

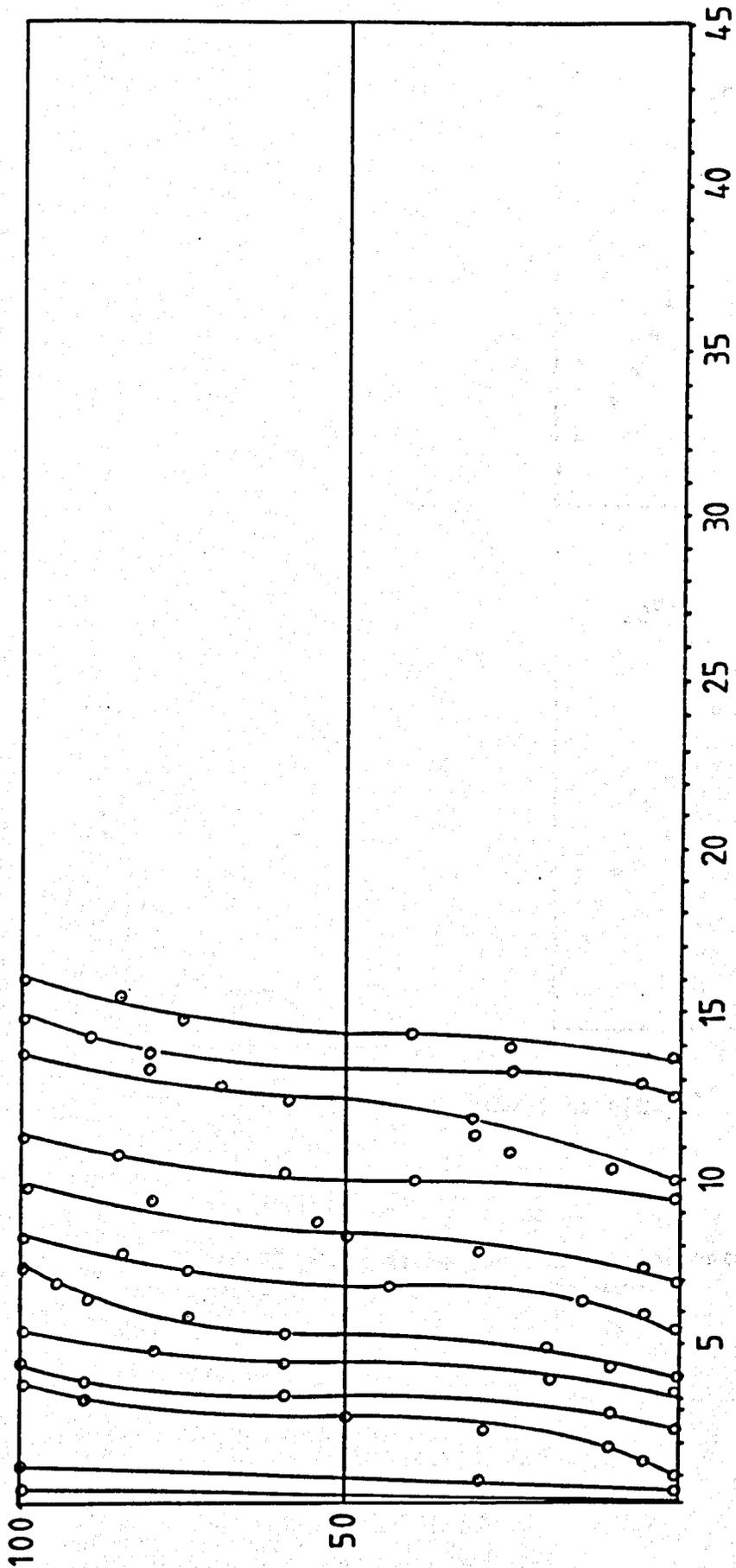


Figure 2.5 Cumulative percent of population beyond a given stage on each sampling date at 20 deg.C, high food level. Curves fitted by eye

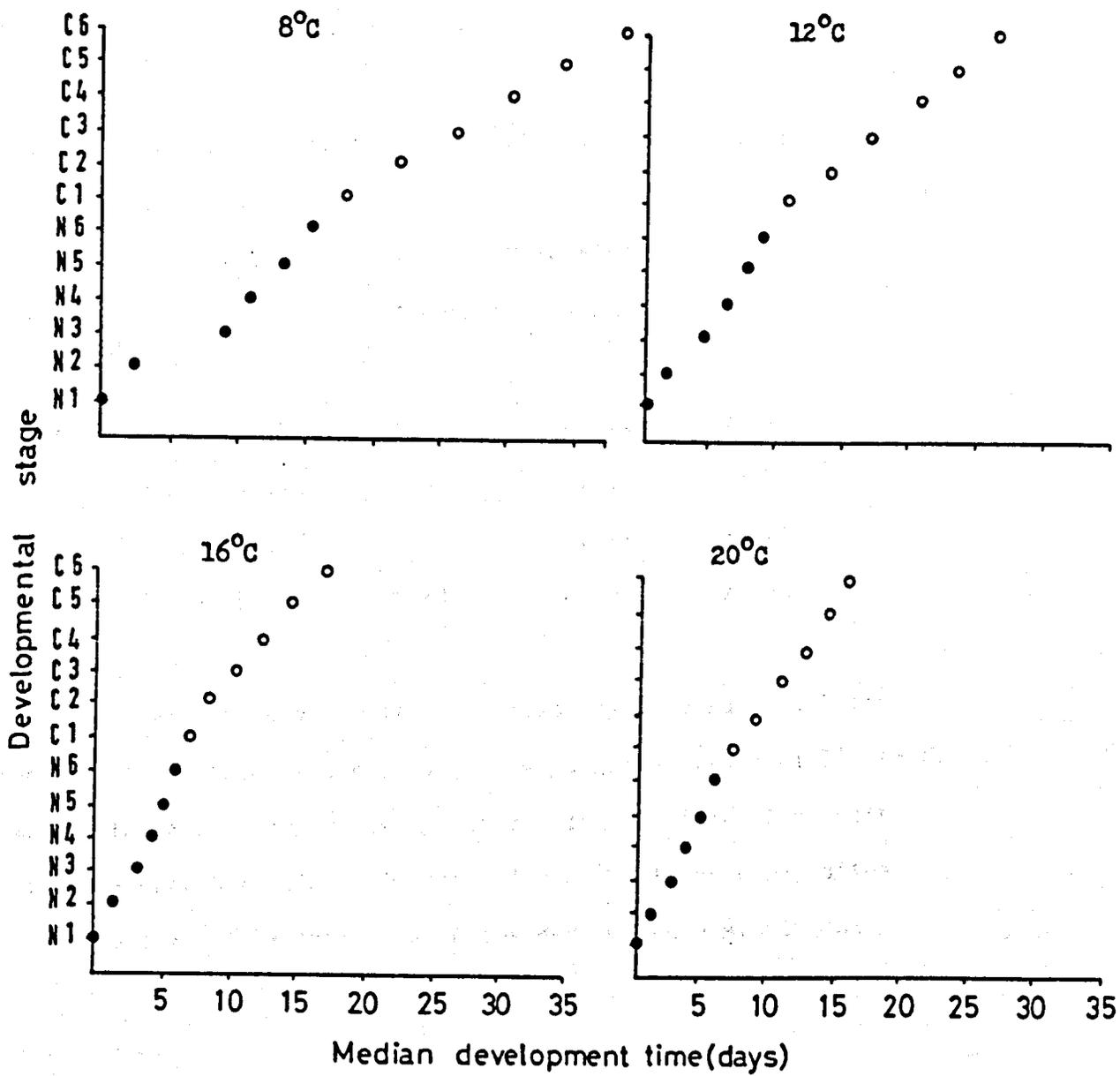


Figure 2.6 Median development times for all developmental stages at four temperatures, high food level treatment

the regression of stage on time was calculated separately for nauplii and copepodites at each temperature (Table).

Table 2.8 Regression parameters: developmental stage versus time

Temp.	Nauplii			Copepodites		
	Constant	Slope	r	Constant	Slope	r
8	-0.326	0.328	92.8%	1.64	0.241	99.9%
12	-0.311	0.595	97.9%	2.64	0.319	99.8%
16	-0.656	0.925	97.1%	3.09	0.471	99.7%
20	0.116	0.853	99.6%	1.83	0.593	99.4%

The slope of each regression has units of stages/day. For nauplii, there is an increase in slope from 8-16 deg.C, with a slight decrease at 20 deg.C. For copepodites, there is a monotonically increasing trend in slope with increasing temperature. Comparison of slopes for nauplii and copepodites at any temperature emphasises that copepodites develop more slowly than nauplii.

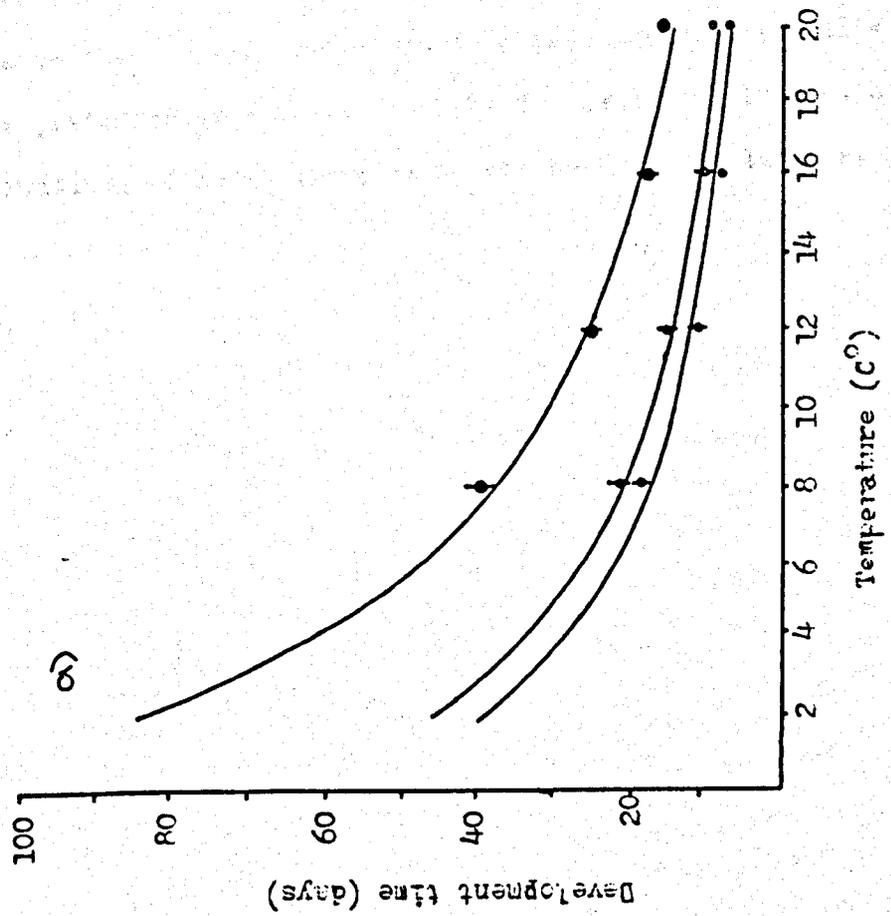
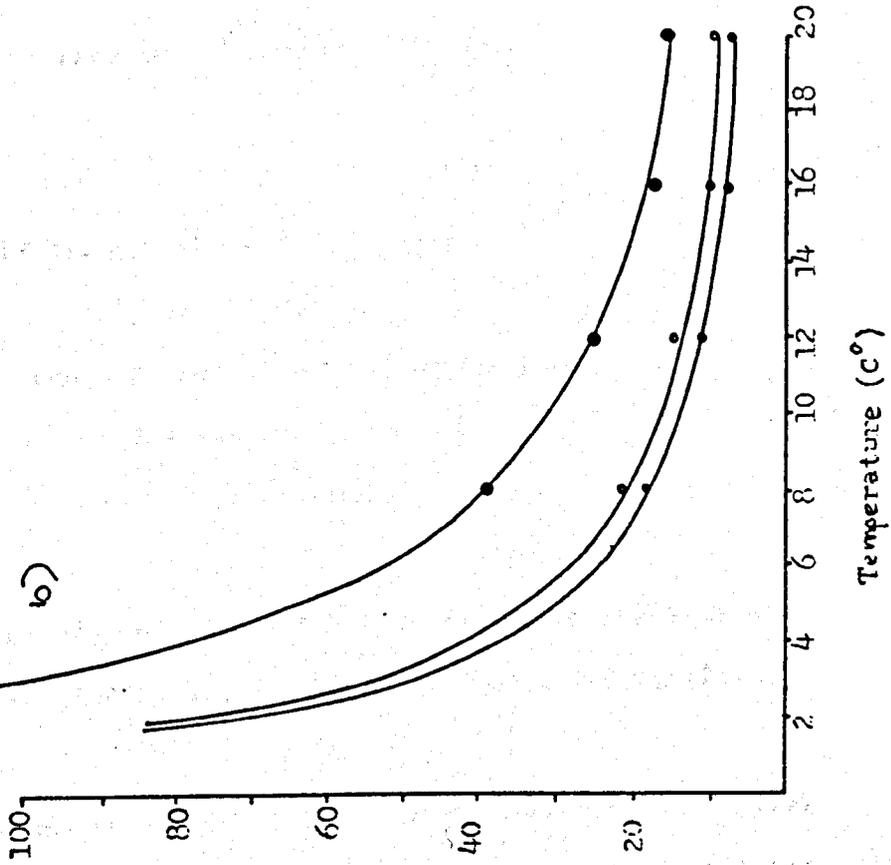


Figure 2.7 Relationship between temperature and development time for nauplii, copepodites and for all stages combined.
 a) fitted using the equation of Bottrell (1975)
 b) fitted using a power relationship

Development rate as a function of temperature

Following Bottrell (1975), equations of the form

$\ln D = a - b(\ln T)^2$ where D = development time in days

T = temperature in deg. C

a, b are constants

were fitted to the development times for nauplii and copepodites and for total development (excluding egg development) (Table 2.9, Fig. 2.7a).

For purposes of comparison, power functions were also fitted (Table 2.9, Fig. 2.7b). The power function equations gave a marginally better fit for nauplii and copepodites (Table 2.9), but appeared biologically less realistic when extrapolated outside the range of experimental temperatures. Bottrell's equation was therefore preferred as a basis on which to predict daily growth rates from field observations of water temperature and mean instar lengths.

Table 2.9 DEVELOPMENT RATE EQUATIONS

A) Based on Bottrell's equation:

- 1) Nauplii $\ln D = 3.76 - 0.215(\ln T)^2$ $r^2 = 93.1\%$
- 2) Copepodites $\ln D = 3.90 - 0.207(\ln T)^2$ $r^2 = 94.6\%$
- 3) Total $\ln D = 4.53 - 0.211(\ln T)^2$ $r^2 = 98.4\%$

B) Power function:

- 1) Nauplii $\log_{10} D = 2.23 - 1.10 \log_{10} T$ $r^2 = 94.3\%$
- 2) Copepodites $\log_{10} D = 2.26 - 1.05 \log_{10} T$ $r^2 = 97.4\%$
- 3) Total $\log_{10} D = 2.55 - 1.07 \log_{10} T$ $r^2 = 98.1\%$

Estimation of daily length increment from field and laboratory observations

Using the equations fitted above, naupliar and copepodite development times were predicted at the ambient *S. Allosa* temperatures on the 9 dates in 1981-2 for which detailed field length data were obtained (Table 1.7). A simplification was introduced by ignoring the fact that, at some times of the year, animals would experience a changing temperature regime.

The coefficients of the regressions of stage on time were obtained (Table 2.8). Estimated field naupliar development times ranged from 7.13d on 7.7.82 to 42.6d on 12.1.82; corresponding copepodite development times for these dates were 8.76d and 49.4d respectively. These values translated into rates of 0.139-0.842 stages/day for nauplii and 0.101-0.571 stages/day for copepodites (Table 2.11).

Field observations relating cephalothorax length to stage (Figs. 2.8a-c) showed a slightly curvilinear relationship, but one which in all cases could be adequately modelled by linear regression (Table 2.12). The regressions yielded coefficients (mm/stage) of between 0.034 (31.5.82, 16.4 deg.C) and 0.049 (2.4.82, 7.6 deg.C) for nauplii and between 0.076 (31.5.82) and 0.101 (11.12.81) for copepodites.

In general, growth per stage, and stage duration, were low at high temperatures and high at low temperatures. An exception to this was the sample for 20.9.82, in which animals of all stages were unexpectedly large (Fig. 1.6).

Table 2.11

DEVELOPMENT TIMES AND RATES OF LENGTH INCREMENT PER STAGE AND PER DAY
FOR 9 DATES IN 1982

DATE	Temp	Dev _n	Dev _c	Rate _n	Rate _c	Inc _n	Inc _c	Daily _n	Daily _c
11.12	7.00	10.03	22.56	0.315	0.222	0.044	0.101	0.0137	0.0224
12.1	0	42.95	49.4	0.139	0.101	0.045	0.091	0.0063	0.0092
3.2	4.06	28.16	32.90	0.213	0.152	0.046	0.096	0.0097	0.0145
2.4	7.56	17.82	21.18	0.337	0.236	0.049	0.099	0.0166	0.0233
31.5	16.40	7.99	9.78	0.751	0.511	0.034	0.076	0.026	0.0388
7.7	18.00	7.13	8.76	0.842	0.571	0.035	0.079	0.029	0.0451
20.9	14.25	9.42	11.46	0.637	0.436	0.046	0.100	0.0289	0.0436
16.11	6.08	21.32	25.17	0.281	0.199	0.043	0.087	0.0119	0.0172
23.12	1.83	39.71	45.81	0.151	0.109	0.044	0.097	0.0067	0.0106

Table 2.12 EQUATIONS RELATING LENGTH TO STAGE

	Nauplii	Copepodites
11DEC	$L = 0.0446 + 0.0435S$ $r^2 = 98.2 \%$	$L = -0.395 + 0.101S$ $r^2 = 95.4 \%$
12JAN	$L = 0.0419 + 0.0453S$ $r^2 = 97.8 \%$	$L = -0.261 + 0.0915S$ $r^2 = 93.2 \%$
3FEB	$L = 0.0448 + 0.0458S$ $r^2 = 97.3 \%$	$L = -0.296 + 0.0956S$ $r^2 = 97.5 \%$
2APR	$L = 0.025 + 0.0492S$ $r^2 = 96.6 \%$	$L = -0.36 + 0.0987S$ $r^2 = 96.7 \%$
31MAY	$L = 0.0588 + 0.0343S$ $r^2 = 98.8 \%$	$L = -0.251 + 0.0761S$ $r^2 = 97.0 \%$
7JUL	$L = 0.0608 + 0.0348S$ $r^2 = 99.4 \%$	$L = -0.268 + 0.079S$ $r^2 = 98.6 \%$
20SEP	$L = 0.0399 + 0.0455S$ $r^2 = 98.1 \%$	$L = -0.346 + 0.1S$ $r^2 = 91.9 \%$
16NOV	$L = 0.0594 + 0.0425S$ $r^2 = 99.5 \%$	$L = -0.259 + 0.0865S$ $r^2 = 98.3 \%$
23DEC	$L = 0.056 + 0.0444S$ $r^2 = 98.8 \%$	$L = -0.339 + 0.0973S$ $r^2 = 97.5 \%$

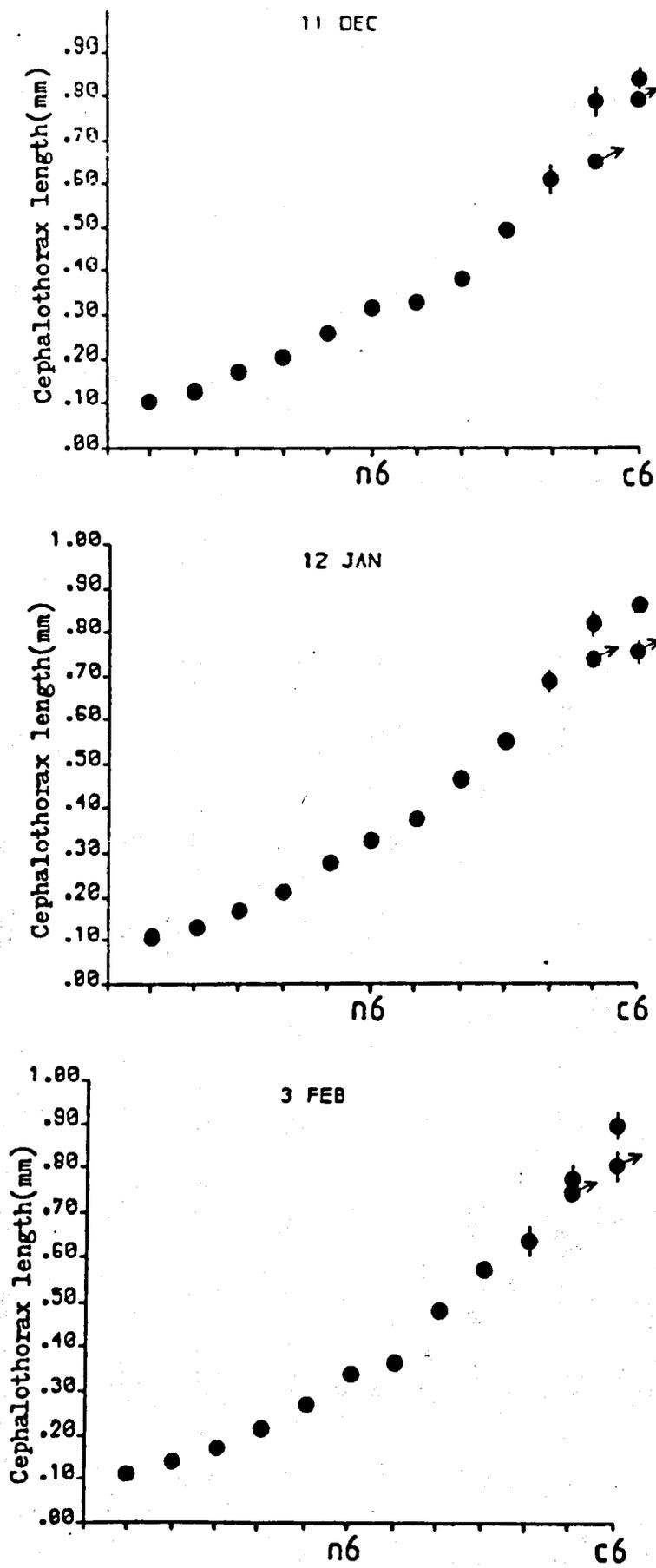


Figure 2.8 a

Relationship between cephalothorax length and stage in E.affinis collected at S.Alloa on 11.12.81, 12.1.82 and 3.2.82

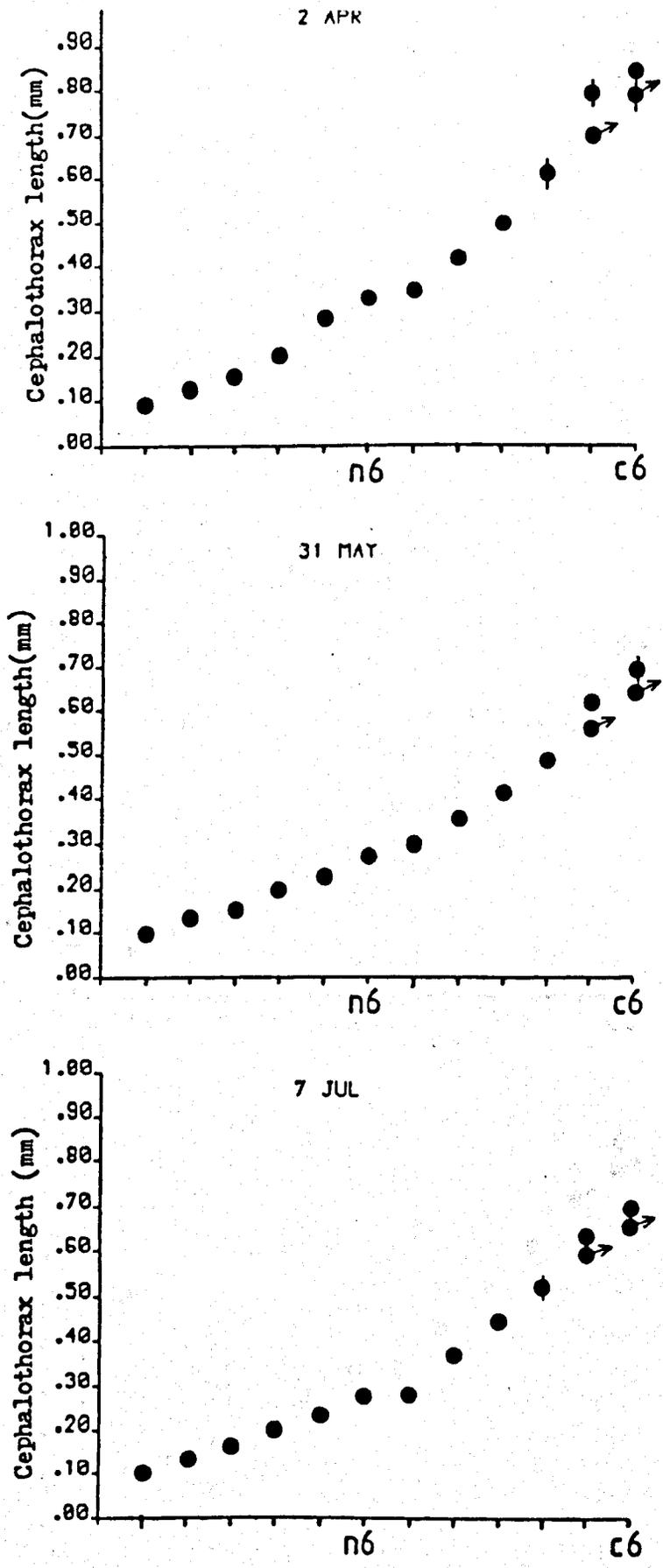


Figure 2.8 b

Relationship between cephalothorax length and stage in E.affinis collected at S.Alloa on 2.4.82, 31.5.82 and 7.7.82

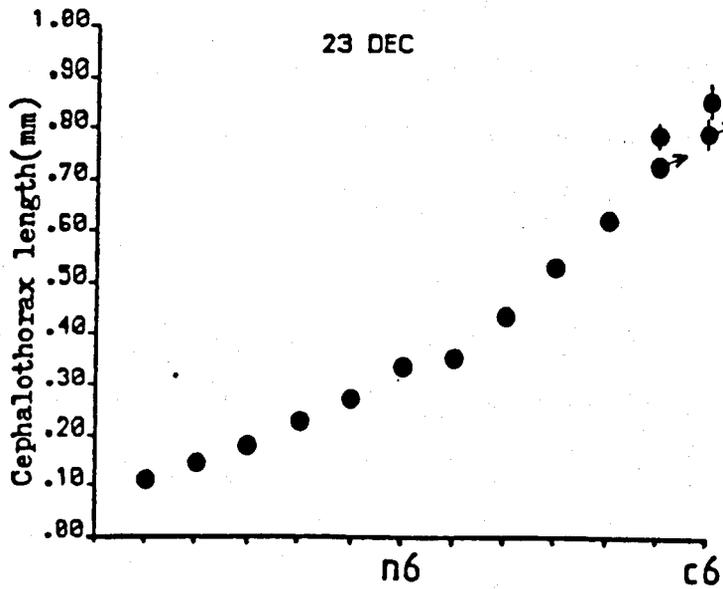
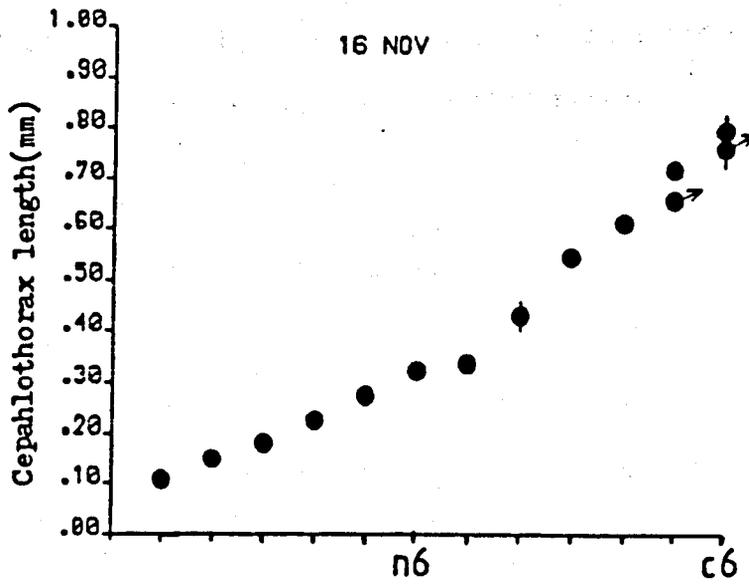
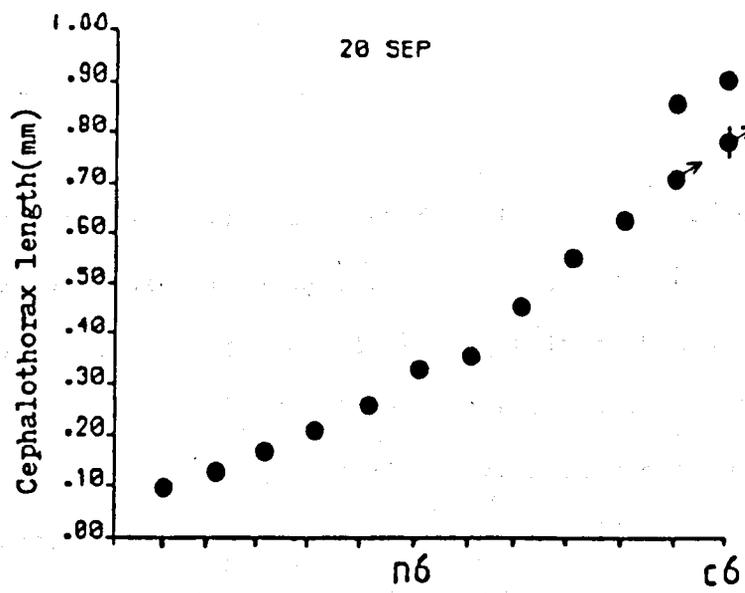


Figure 2.8 c

Relationship between cephalothorax length and stage in *E.affinis* collected at S.Alloa on 28.9.82, 16.11.82 and 23.12.82

Daily length increment (mm/day) was estimated from the product of development rate (stages/day) and growth rate (mm/stage) (Table 2.11, Fig.2.8). This reveals that, although copepods achieved a greater final length in each stage at low temperatures (with the exception of 20.9.82), growth rates were considerably higher in spring and summer as a consequence of the temperature-enhanced development rates. Highest growth rates were predicted for 20.9.82 for nauplii (0.029 mm/day), and 7.7.82 for copepodites (0.045 mm/day). Lowest growth rates were predicted for 12.1.82, and were, for nauplii and copepodites respectively, only 22% and 21% of the highest predicted rates.

Chapter 3

Predation by Neomysis integer on Eurytemora affinis

Predation of *Neomysis* on *Eurytemora affinis*

Between 29.9.83 and 31.10.83, a series of experiments were conducted to investigate the effectiveness with which Neomysis could prey on Eurytemora. These comprised;

- a) the investigation of the relationship between mysid length and predation rate
- b) the generation of a functional response for adult mysids by determining predation rate at a range of prey densities representative of those observed in the Forth estuary
- c) the investigation of the effect of the absence of light and the presence of natural suspended particulate material on predation rates in adult mysids.

All experiments were carried out at 15+/- 1 deg.c and at 10 +/-1 ppt. Water for each experiment was made up from S.Alloa water collected on high tides, filtered to 1.2 um, and diluted as necessary with fresh(0%) Forth river water similarly filtered. An exception was the investigation of the effect of suspended particulate material on predation rate, when the suspended solids content of the medium was adjusted to approximately 65 mg/l. All experiments were carried out over 24h in a 12:12 LD lighting cycle, with the exception of the test of predation rate in the dark. Illumination, when present, was diffused and attenuated by expanded polystyrene sheets to approximately 1.2 Lux.

Experiments in b) and c) used adult mysids of between 14 and

17mm in length, which had been held in filtered 10 ppt estuary water for 24 h prior to introduction to the test vessels. Mysids used in a) had been similarly treated, but ranged in size from 5.04 to to 19.0 mm in length. Only mysids which had not moulted in the 24h prior to testing were used, and only one mysid was introduced to each test vessel. All trials were conducted in acid-washed glass beakers, loosely covered to minimise evaporation losses.

Preliminary tests were conducted under less well-controlled circumstances to establish whether or not Neomysis could capture Eurytemora under laboratory conditions

Collection of experimental material

Copepods, mysids and water collected from S.Alloa on high tides between 26.9 and 27.10. Additional water was collected on each occasion from Stirling bridge. Animals were collected using a hand-net equipped with a transparent cod-end. Following each net sweep, the contents were washed gently into the cod-end and the cod-end detached and decanted through a 1mm mesh (through which copepods passed) into a polythene aspirator containing 5 litres of ambient water. Juvenile and adult mysids retained on the mesh were washed gently into a separate and similar container. Inspection of the contents of the cod-end permitted the size of the catch to be approximately estimated.

The contents of the aspirator were placed in a cool-box and transported to the laboratory within 1 hour of collection.

Pre-treatment and exposure of mysids

a) effects of size on predation rate: 29.9.83

The contents of the aspirator were mixed thoroughly, and a 1-litre subsample rapidly taken to obtain a sample of approximately 30 mysids of varying sizes. Half of these animals were gently transferred individually with a wide-bore pipette into beakers containing 100 ml filtered habitat water, and the time noted. The remaining mysids were placed in 5l of unfiltered habitat water for 24h. During this period, sufficient adult E.affinis for the experiment were sorted. Damaged individuals were rejected, and 1500 intact and active specimens were placed in groups of 100 into 15 200ml polystyrene beakers containing filtered 10ppt estuary water. These beakers were placed in a C.T. room at 15 deg. C. A further 1500 adult E.affinis were placed in 10 l unfiltered estuary water (10 ppt) and held in the same room. After 24h, mysids held in filtered water were examined, and active, un-moulted animals were transferred individually, at 10 min. intervals, to 21 beakers each containing 100 adult E.affinis. The mysids held in unfiltered water were transferred individually into 100 ml of filtered water. Staggering the initiation of the predation trials allowed sufficient time to terminate each trial without affecting the duration of any other, although since all trials were conducted in the same C.T. room there was a consequent variation in the lighting history of successive trials. During the first set of trials, the remaining 1500 E.affinis were sorted into groups of 100 and held in filtered 10 ppt estuary water.

Each trial was terminated 24h after initiation, by decanting the contents of the beaker through 1mm mesh into a 100ml container with 69 um mesh- covered holes near the base. Neutral red stain (1:200000, Dressel et al, 1972) was added to the material retained, which was stained for 30 min. and then preserved in acidified 4% Steedman's solution and transferred to a Beatson jar for subsequent examination. Staining served to assess the degree of mortality in the prey sample, and thus to indicate the extent to which results may have been biased by "uncontested" capture. It was expected that mortality due to unsuccessful attacks would be evident from physical damage sustained by such copepods during the attack.

Following the termination of the first set of trials, the 21 experimental beakers were rinsed with filtered test water (10 ppt) and refilled. 100 adult E. affinis were added to each beaker, and the second batch of mysids exposed to prey in the same manner as were the first batch. Two controls with 50 prey but without predator were run in conjunction with each batch.

b) Estimation of functional response

During the period 2.10.83 to 22.10.83, trials were conducted at densities of 10,25,50,100,200,300 and 500 prey/l. Each treatment was replicated five times, with two controls, and each treatment tested on 5 separate occasions. Pre-treatment of mysids was as described above, except that individuals were briefly restrained in a small trough and measured to the nearest millimetre. For each treatment, five mysids between 14 and 17mm in length were selected and held in filtered water for 24h. Adult E.affinis were sorted during the starvation period and added to the experimental beakers just before the mysids.

Beaker volume differed between treatments. At 10 prey/l 5 litre beakers were used (50 prey per mysid). At 25 prey/litre, tests were replicated in both 5 and 2 litre beakers, and at 50 prey/litre in both 2 and 1 litre beakers. The remaining prey densities were tested in 1 litre beakers. All beakers were filled to their nominal capacity. Mysids were exposed to prey for 24h, and replicates were initiated at 10-minute intervals to eliminate variation in exposure period due to the time taken to terminate each one.

At the end of the exposure period, the vessel contents were decanted as described above and the contents preserved.

c) Predation in the dark and in the presence of suspended sediments

14-17mm mysids were obtained on 28.10 for the investigation of the effects of darkness and on 31.10 for the investigation of the effects of the presence of suspended particulate material. Mysids were measured, held in filtered water for 24h and the tests initiated as described above, with 5 replicates and two controls per treatment.

Predation in the dark was measured at 50 and 100 prey/litre in 2 litre beakers filled to nominal capacity. Mysids were exposed at these concentrations for 24h in a light-tight CT room at 15 deg.

C.

Predation in the presence of detritus was tested at 25,50 and 100 prey/litre, also in 2 litre beakers. Habitat water, adjusted to 10 ppt, was screened through a 69 um mesh, and 3 250 ml subsamples filtered onto tared Whatman GF/C filters and dried for 24h at 60 deg. C. The mean suspended solids content was 65.08 mg/l, which was considered sufficiently representative of estuarine conditions to require no adjustment. Mysids were exposed for 24h. The beakers were not mixed during the exposure period, and the particulate material gradually settled out on the bottom. Each replicate was observed at intervals during the exposure period to obtain an impression of the effect of this sedimented layer on the behaviour on both mysids and copepods.

In both experiments, adult E.affinis were, as above sorted during the pre-exposure period. Both sets of trials were terminated as described above.

Sorting and preparation of copepods

The experiments described above required a total of 13875 adult E.affinis. The constraints of time imposed in setting up each treatment demanded a rapid, efficient and gentle method of sorting.

Following each collection, subsamples from the collection were cumulatively concentrated in a 100ml polystyrene container with 69 um-mesh-screened holes near the base. When several hundred had been concentrated into about 15 ml of estuary water, they were aspirated gently into a sorting device consisting of a Pasteur pipette with the final 2 cm bent to 120 degrees, attached via 20cm of 3mm internal diameter polythene tubing to a 20ml thumbwheel-controlled pipette filler. This device permitted precise control of the movement of water into and out of the pipette tip.

The pipette tip was transferred to a 90mm Petri dish which had a divider glued in place across the diameter. The final two 2cm of the tip was placed flat on the bottom of the Petri dish, below the surface of filtered estuary water, and the position of the dish adjusted so that the 2cm section was within the field of view of a Wild M5 stereo dissection microscope. The refractive index of the water and of the pipette glass were sufficiently close that the contents of the pipette tip could be resolved clearly enough to identify individual copepods to species and to

stage. The contents of the device were expressed slowly into one half of the dish. When an adult male or female Eurytemora approached the end of the pipette, the pipette filler was manipulated until the individual was at the pipette end. The pipette was raised and the individual ejected into a drop at the pipette tip, which was then dipped gently and briefly into the water in the other half of the Petri dish. The pipette was transferred back to the original side of the division, and the sorting process continued; unwanted copepods were expressed directly without manipulation. Given the largely monospecific nature of the samples from S. Alloa, it proved possible to sort in excess of 1000 adult E. affinis per hour

Copepods were transferred in groups of 25, 50 or 100 into 100ml beakers of filtered 10 ppt estuary water and held in dim light at 15 deg. C until required. For each set of trials, an additional 25 copepods were held in filtered water; these animals were used to replace any which died or became moribund during the holding period and ensured that only active, apparently healthy specimens were used as prey.

Evaluation of results

The preserved specimens from each trial replicate were concentrated into 2ml of fresh 4% Steedman's solution made up with 10 ppt filtered estuary water. This volume was pipetted into a Bogarov counting tray, and the copepods counted. Each was examined for signs of damage, and any which had not taken up the Neutral red stain (and were therefore dead at the end of the trial) were noted.

Small mysids were placed in the Bogarov tray and the length from rostrum tip to telson end measured with a calibrated eyepiece graticule to 0.1mm. Larger mysids were placed on a piece of graph paper and their length similarly measured to 0.5mm.

Faecal pellets produced by mysids during trials were examined and their contents qualitatively assessed.

The effect of mysid size on predation rate was evaluated from the regression of rate in prey/mysid/day on mysid length in mm.

For the remaining experiments, feeding rate was calculated as clearance rate (Fulton, 1982a; Frost, 1972, 1975; Cooper and Goldman, 1980)

$$Cr = (-\ln(N_t/N_o)V)/(N_p T) \quad (\text{equation 1})$$

Where Cr = clearance rate (l/h)

No = initial(control) number of prey

Nt = number of prey at time T (h)

V = volume of experimental vessel (l)

Np = number of predators

The relationship between clearance rate and prey density was tested by analysis of covariance (ANCOVA) in which clearance rates were normalised by $\log(x+1)$ transformation, as the variances were found to be heterogeneous by Bartlett's test. The model partitioned variance between prey density and blocks(days), with mysid length as a covariate.

Predation rate was calculated as:

$$P = (N_0 - N_t) / TNp \quad (\text{equation 2})$$

Although Frost(1972), Landry(1981) and Williamson and Butler(1986), inter alia, have suggested the use of mean, rather than initial, prey density in the representation of predation relationships, Marin et al (1986) have pointed out that mean prey density is not independent of predation or clearance rate. It is thus incorrect to determine a functional response based on mean density. Further, the use of mean prey density invalidates the replication of treatments and means that there is no independent estimate of error in clearance rate for any treatment.

Clearance rate was also calculated following Marin et al(1986) as

$$Cr = V((Co-Ct)/Co) \quad 1/h \quad (\text{equation 3})$$

where V = vessel volume

Co, Ct = initial(control) and final prey
densities respectively

This equation is appropriate when clearance rate is not constant
but declines with increasing food concentration.

Ingestion rate may be calculated from equation 3 simply as

$$I = CrCo$$

Results

Relationship between mysid size and predation rate

All copepods recovered from experimental vessels in this experiment stained strongly with Neutral red, and were presumed to have been alive and active throughout the experimental period. Two mysids moulted during the exposure period, and these results were discarded.

A linear relationship adequately described ($r=0.93$, $p<0.01$) the observed increase in predation rate (copepods/mysid/day) with mysid length (Fig.3.1, Table 2.1). Since neither variable was measured without error, and the size distribution of mysids must be regarded as truncated, a functional or geometric mean regression was calculated (Ricker, 1973):

$$y = -11.59 + 2.60x$$

where y is predation rate (copepods/mysid/day)

x is mysid length (mm)

The regression line intercepted the x-axis at a mysid length of 4.45mm. Mysids below this length did not appear to be able to feed effectively on adult Eurytemora.

Predation rates for mysids in the 14-17 mm size range used in subsequent experiments clustered between 25 and 33 copepods/day at a prey density of 50/litre. The highest rates were observed in the two largest mysids, which captured 39 and 40 prey respectively during the 24h exposure period. This

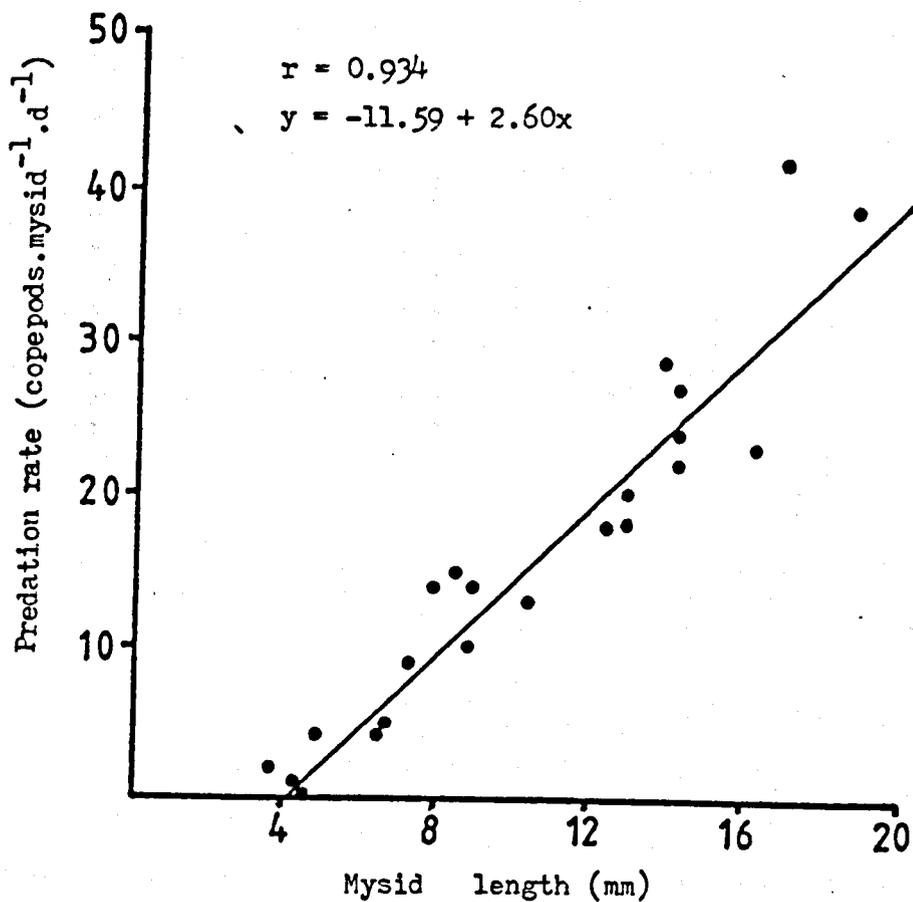


Figure 3.1

Functional regression of mysid length on predation rate; correlation coefficient for least-squares included as an approximate indication of the strength of the relationship

Table 3: The relationship between mysid length and predation rate at a prey density of 50 prey per litre

Mysid length(mm)	No. prey recovered	Control recovery	No. prey taken	No. prey moribund
5.04	46	(51,50)	4	0
3.82	48		2	0
4.60	51		0	0
4.39	49		1	0
6.60	46		4	0
9.00	40		10	0
7.92	36		14	0
7.48	41		9	0
10.51	37		13	0
9.07	36		14	0
6.77	45		5	0
8.64	35		15	0
14.50	28	(50,50)	22	0
12.50	32		18	0
16.50	27		23	0
13.00	37		13	0
19.00	21		29	0
17.00	10		40	0
13.00	29		21	0
14.00	22		28	0
13.00	26		24	0
13.50	28		22	0

was equivalent to a clearance rate of 1.6 l/mysid/day.

Comparison of the mysid size range used here with the data of Astthorsson and Ralph (1984) indicate that the greater part of the normal size spectrum of Scottish Neomysis (~3mm to >16mm) was sampled, but that the sample almost certainly contained representatives of two generations. The larger mysids are likely to have belonged to the summer generation, while the smaller (<10mm) mysids will have been members of the autumn-born overwintering generation.

Functional response: the relationship between prey density and predation rate

In all replicates, uneaten copepods stained strongly with Neutral red, and, as above, it has been assumed that all constituted normally-available prey up to the end of the exposure period. None of the 35 mysids used moulted during exposure; Assthorsson and Ralph (1984) reported that the intermoult period for mature mysids is between 12 and 18 days, so moulting would not be expected to be a frequent occurrence.

Mysid faecal pellets recovered from experimental vessels were without exception loosely-packed and contained identifiable copepod remains.

Mean raw predation rate ranged from 24.2 copepods/day at 10 prey/l to 127.4 copepods/day at 500 prey/l (Table 3.2, Fig. 3.2). Predation rate increased monotonically with prey density up to 115/day at 200 prey/l, declined slightly at 300 prey/l, and increased to 127/day at a density of 500/l.

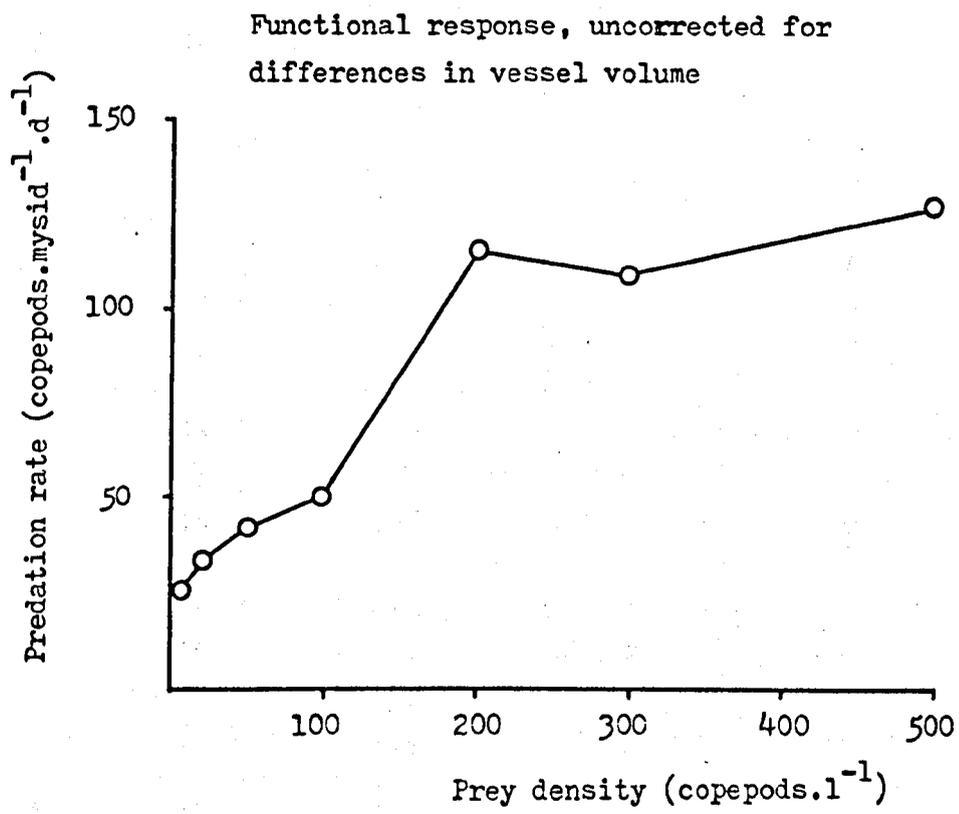


Figure 3.2

Table 3.2 Mysid predation on E. affinis at a range of prey densities; number of prey recovered, number of prey taken, and predator length.

Prey density	Vessel volume(l)	Mysid length(mm)	No. prey recovered	Control recovery	No. prey taken	No. dead
10	5	16.0	30	(52,49)	20	0
		16.5	27		23	0
		16.0	25		25	0
		15.5	22		28	0
		16.0	25		25	0
25	2	16.5	31	(50,50)	19	0
		15.0	30		20	0
		15.5	33		17	0
		17.0	27		23	0
		16.0	34		16	0
25	5	16.5	93	(123,124)	31	0
		15.5	89		35	0
		17.0	87		37	0
		16.5	92		32	0
		15.0	79		45	0
50	1	16.5	8	(50,51)	42	0
		14.0	30		20	0
		14.5	21		29	0
		14.5	22		28	0
		15.0	26		24	0
50	2	15.0	55	(100,100)	45	0
		15.5	55		45	0
		15.5	76		24	0
		16.0	53		47	0
		15.0	51		49	0
100	1	14.0	54	(100,100)	46	0
		14.5	57		43	0
		15.0	54		46	0
		15.0	37		63	0
		14.5	48		52	0
200	1	15.5	80	(201,199)	120	0
		16.5	88		112	0
		16.0	82		118	0
		16.5	90		110	0
		16.0	85		115	0
300	1	15.5	189	(300,302)	112	0
		14.0	195		106	0
		16.0	186		115	0
		14.5	187		114	0
		14.5	191		110	0
500	1	14.5	349	(497,501)	150	0
		14.0	375		124	0
		14.0	386		113	0
		14.0	367		132	0
		13.5	381		118	0

Table 3.3 Clearance rate of mysids feeding at a range of prey densities; rates calculated using models which assume a) constant clearance rate with declining prey density and b) decreasing clearance rate with increasing prey density. Values are mean 1/h, 95% confidence intervals in brackets

		Prey density								
		10	25	50	100	200	300	500		
		Vessel volume								
		5	5	2	2	1	1	1	1	
a)		3.38 (0.65)	1.70 (0.37)	0.96 (0.26)	1.11 (0.36)	0.95 (0.59)	0.70 (0.21)	0.86 (0.05)	0.46 (0.03)	0.30 (0.05)
b)		2.42 (0.33)	1.48 (0.22)	0.76 (0.13)	0.84 (0.23)	0.57 (0.20)	0.50 (0.09)	0.54 (0.08)	0.37 (0.01)	0.25 (0.02)

Table Mean predation rates of mysids feeding at a range of prey densities (copepods/mysid/day);
a) actual numbers taken in 24h
b) numbers corrected to unit vessel volume

		10	25	50	100	200	300	500		
		Vessel volume								
		5	5	2	2	1	1	1	1	
a)		24.2 (3.4)	36.0 (6.4)	19.0 (3.1)	42.0 (11.7)	28.6 (9.5)	50.0 (.92)	115.0 (4.7)	111.0 (4.1)	127.4 (16.6)
b)		4.8 (0.7)	7.2 (1.3)	9.5 (1.6)	21.0 (5.9)	"	"	"	"	"

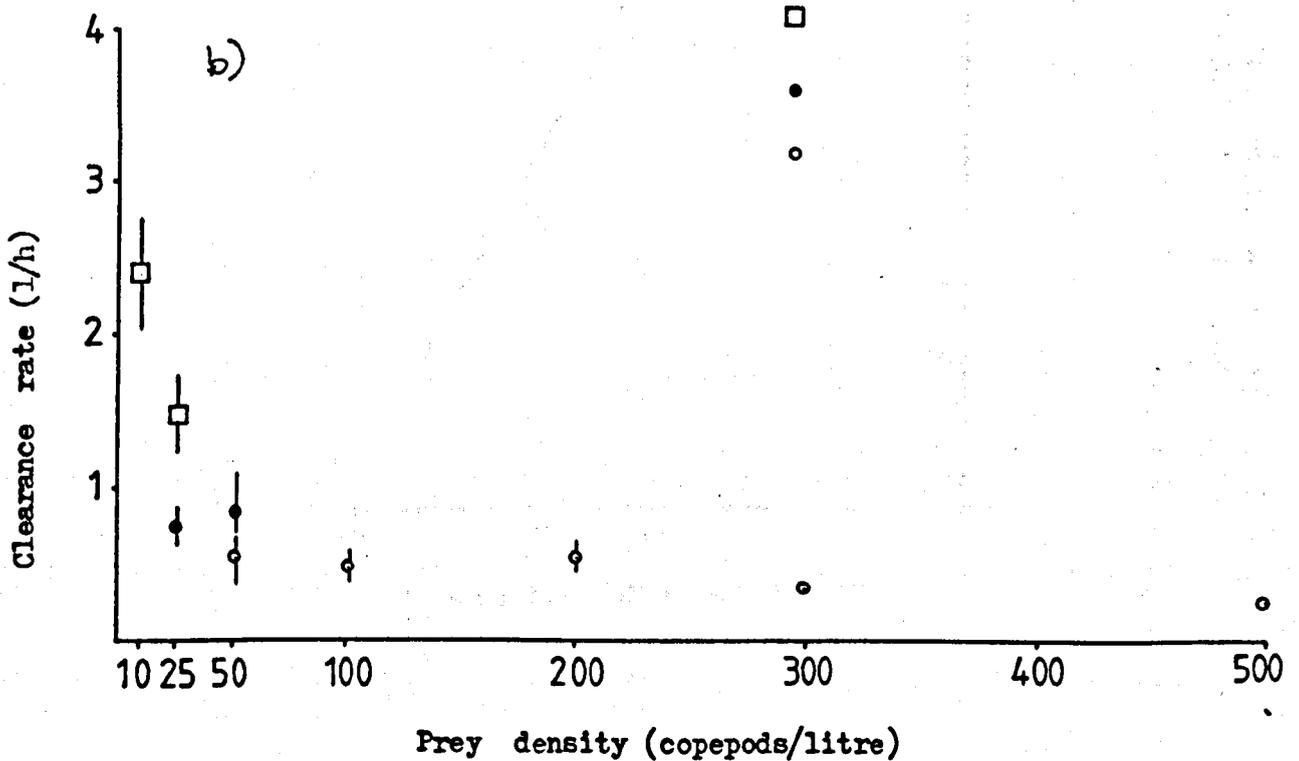
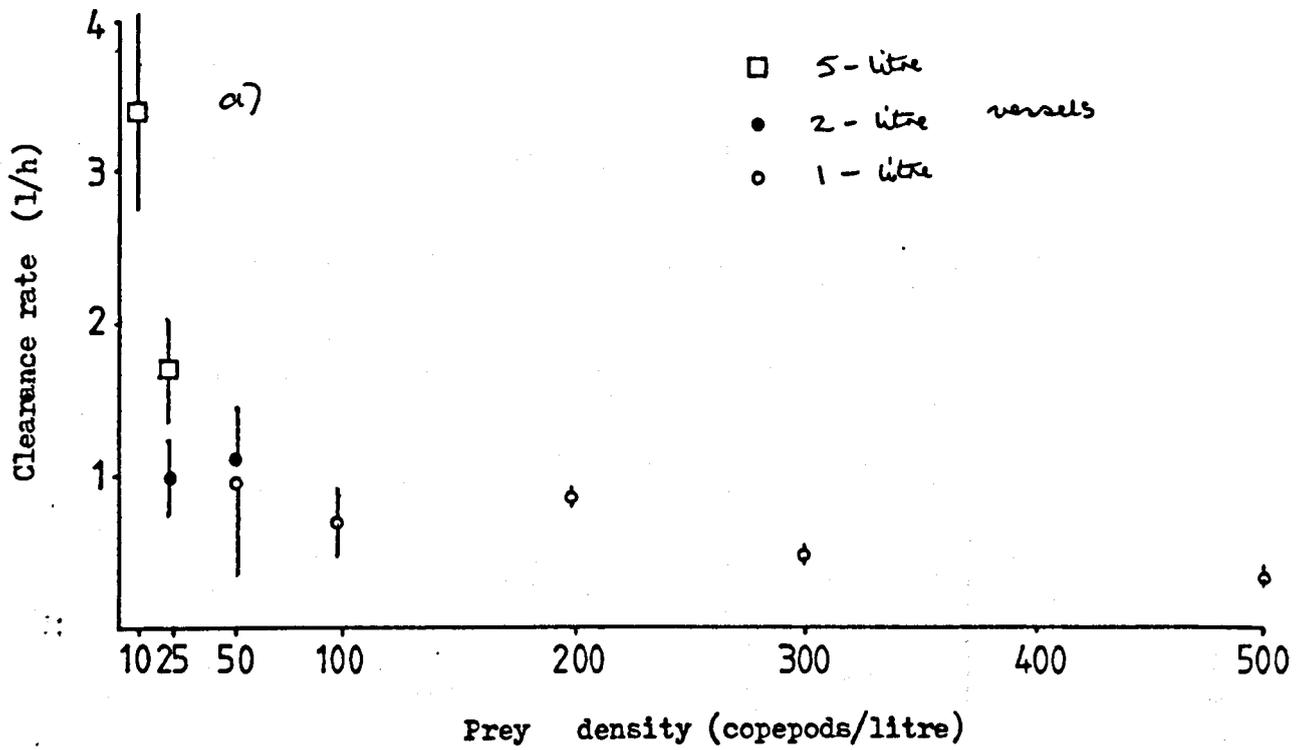


Figure 3.3 The relationship between clearance rate (l/mysid/day) and prey density (no./l) in vessels of different volumes
 a) clearance rate calculated using the equation of Frost (1972)
 b) clearance rate calculated using the equation of Marin et al (1986)

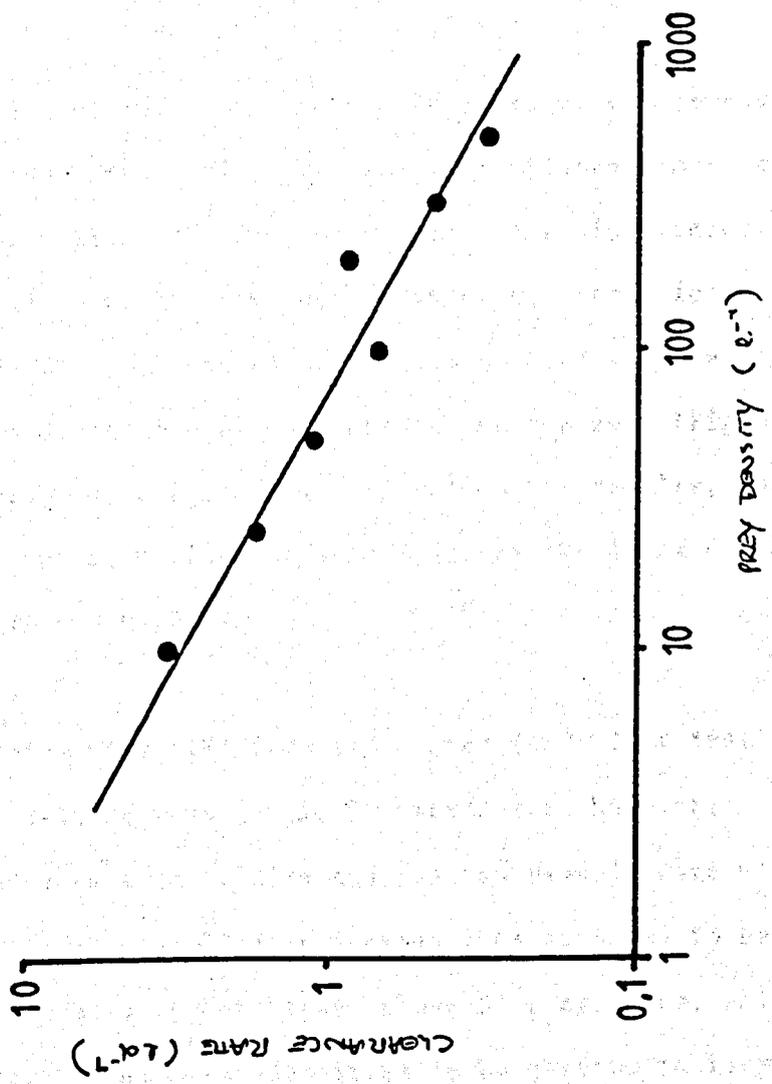


Figure 3.4

The relationship between log10 clearance rate and log10 prey density. Line fitted by eye

Clearance rates were calculated using both the conventional exponential expression (e.g. Frost, 1972) and that of Marin et al (1987) (Table 3.3, Figs. 3.3a,b). Rates based on the latter equation were consistently lower at any given prey density than those based on the former; on both bases, however, rates exhibited a declining curvilinear relationship with prey density, characteristic (Fulton 1982) of a Type II functional response (Holling, 1965).

The curvilinear nature of the relationship between clearance rate and prey density is emphasised if \log_{10} clearance rate is plotted against prey density (Fig.3.4).

Because the experiments were carried out on a number of days, and because mysid length differed between treatments, analysis of covariance was carried out to a) determine whether either of these covariates had a significant effect on the results and b) to correct the estimates of clearance for any effects that were detected. The analysis was conducted on $\log(x+1)$ -transformed data because of the obvious dependence of the variance on the mean (Fig.3.3).

Neither day nor mysid length had a significant effect on the results, and only the treatment effect was significant (Table 3.4). In the light of this result, clearance rates were not adjusted.

At 25 prey/l, clearance rates were significantly higher ($p < 0.01$, t-test) in 5 litre vessels than in 2-litre vessels. At 50 prey/litre, however, differences between clearance rate in 2-litre and 1-litre vessels were not statistically significant. ($p > 0.05$). Clearance rates thus appeared to be independent of vessel volume at prey densities above 50 prey/litre, while mysid foraging activity appeared at lower densities to be greater in larger vessels than in smaller vessels.

Under circumstances where clearance rate is independent of vessel volume, Fulton(1982) has pointed out that prey density will decline faster in smaller

vessels; consequently, predation rate will be higher, for a given clearance rate, in larger vessels. This observation has been used, following Fulton (1982) to generate a functional response standardised to unit volume (Figs.3.5,3.6).

The results of standardisation (computing predation rate by holding $v = 1$ in the equations of Frost (1972) and Marin et al 1987) are indicated in Table 3.3: values for larger vessels are substantially reduced, and differences between different-sized vessels at 25 and 50 prey/litre also much reduced.

The functional response was modelled in two ways. Firstly, a rectilinear model, frequently applied to invertebrate predators (Cooper and Goldman 1979), fitted by eye (Fig.3.5). A chi-squared goodness-of-fit test yielded a value of 8.64 ($p < 0.01$). Secondly, an attempt was made to fit Holling's (1965) disc equation (Fig.3.6):

$$N_a = \frac{aN T}{1 + aN T_h}$$

where N_a = no. of prey eaten

a = instantaneous coefficient of attack

N = no. of prey available

T_h = handling time (d)

T = duration of experiment (d)

This yielded an estimate of 0.873 for a and of 6.97 minutes for T_h . The curve corresponding to this solution was generated by a computer plotting routine (GINOGRAF) (Fig.3.6). The chi-squared value was 8.06, indicating an adequate fit. The 'disc' model suggests that predation rate will increase at a decreasing rate up to prey densities in excess of 1000/litre; this

Functional response of Neomysis feeding on E.affinis:
rates standardised to unit volume

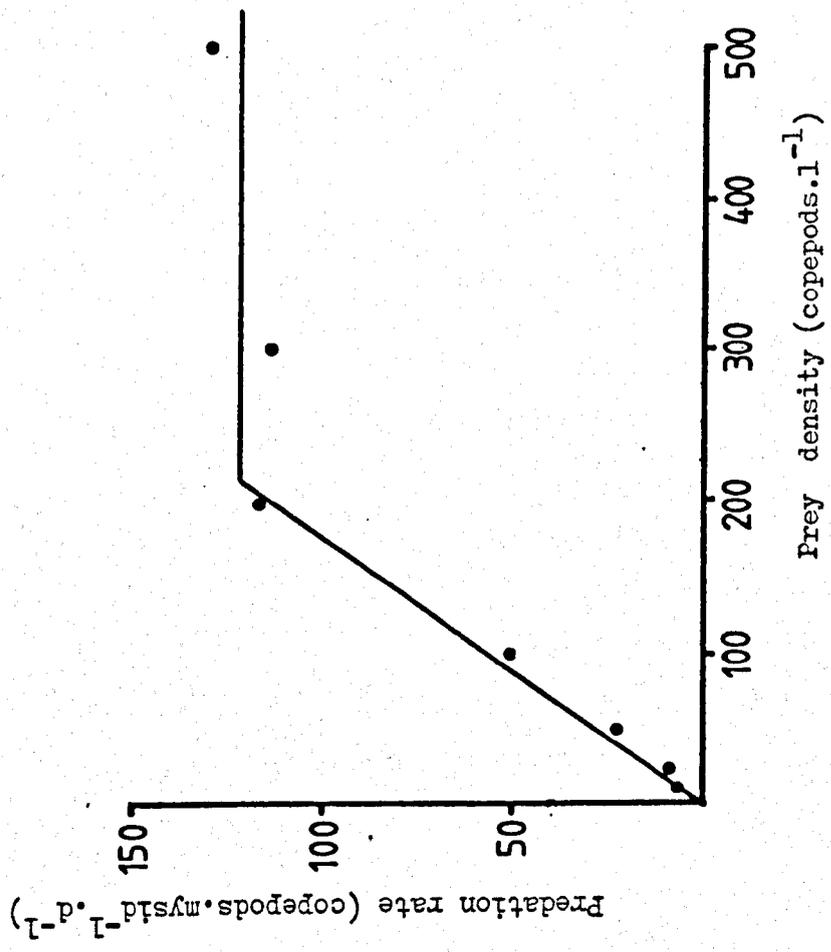


Figure 3.5

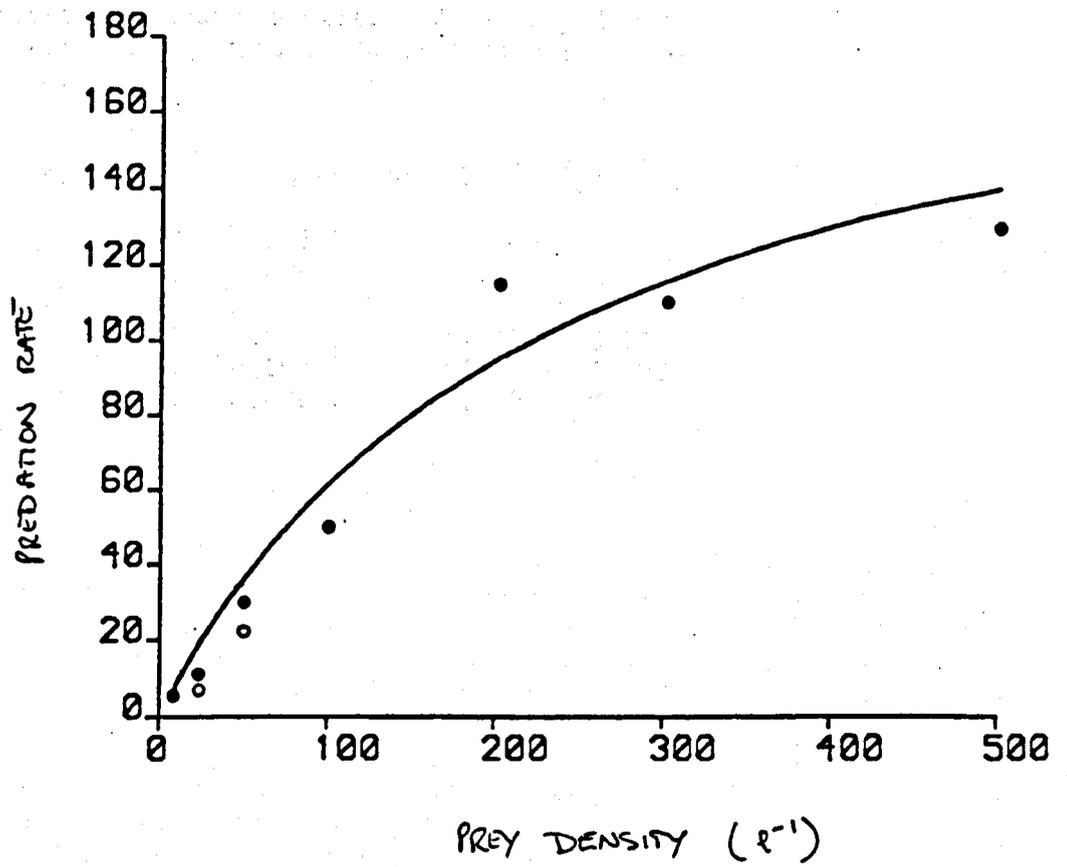


Figure 3.6 'DISC' EQUATION : TYPE II CURVE

Table 3.5 Mean clearance rates (1/h and 95% confidence intervals) of mysids feeding at 50 and 100 prey/litre in the dark and at 25,50 and 100 prey/litre in the presence of detritus Clearance rates calculated using exponential equation.

	Prey density	Clearance rate(1/h)	95% C.I.
Dark	50	1.28	0.39
	100	1.41	0.20
Detritus	25	0.98	0.17
	50	0.76	0.18
	100	0.67	0.10

Table 3.4 Analysis of covariance of $\log(x + 1)$ -transformed clearance rates measured at a range of prey densities; variance partitioned by prey level and blocks(days) with predator length as a covariate.

Source of variation	df	Mean square	F	Significance
Residual	23	0.00163		
Regression (length on rate)	1	0.00668	4.09	NS
Constant	1	0.02310	14.16	0.01
Prey density	6	0.10822	66.37	0.001
Blocks(days)	4	0.00187	1.15	NS

is approximately the maximum abundance observed in UK estuaries (Burkill, 1982) and is almost double the highest abundance recorded for Eurytemora in the Forth (Roddie, 1980). At 1000 prey/litre, predation rate is predicted to be 167 copepods/day, and this may be considered the effective maximum rate likely to occur in the upper Forth estuary. It should be noted that in fitting the above curves, predation rates at 25 and 50 prey/litre were those derived from experiments in the larger of the two vessel sizes used.

Predation in the presence of detrital material

No mortality was observed amongst unpredated copepods in this experiment. Mysid faecal material recovered from the experimental vessels was dark in colour, and contained considerable amounts of compacted material. By virtue of the contrast between these faeces and those produced in the previous experiment, it was inferred that the compacted material was of detrital origin. The faeces also contained identifiable copepod remains.

Since the vessels were unstirred throughout the exposure period, the mysids had clearly spent some of their time foraging on the vessel bottoms. This inference was supported by direct observation; although a formal time budget was not constructed, intermittent viewing indicated that time was apportioned between bottom-feeding and active swimming. It was also observed that a variable proportion of copepods were located at the sediment surface whenever viewing took place, so it is not clear whether or not ingestion of detritus was simply a consequence of foraging for these animals.

Predation rates (Table 3.7) and clearance rate (Table 3.6) were similar to those at the same prey densities in the absence of detritus. Predation ranged from a minimum of 15/day at 25/litre to a maximum of 54/day at 100 prey/litre.

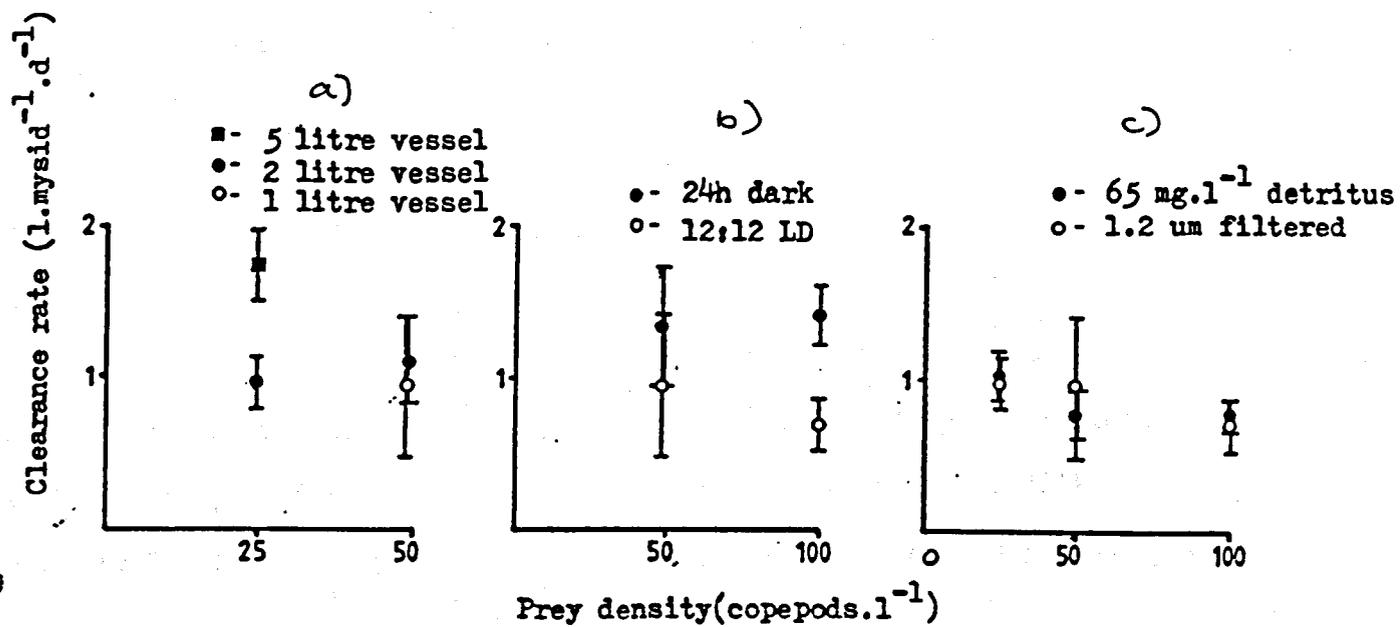


Figure 3.7

The effects of vessel size (a), absence of light (b) and presence of detritus (c) on the clearance rate of *N.integer* feeding on *E.affinis*.

Mean clearance rate in the presence of detritus was compared statistically at each prey density with clearance rate in filtered seawater. F-ratios for each pair indicated that variances were homogeneous, so t-tests were performed on untransformed values. At no density were significant differences apparent ($p > 0.05$, Fig.3.7c). Foraging on copepods did not therefore seem to be affected by the presence of a potential alternative food source.

Predation in the absence of light

As with the experiments reported above, no copepod mortality other than directly due to predation was observed. Predation rates at 50 prey/litre ranged from 21-41/day, and at 100 prey/litre from 70 to 83 prey/day (Table 3.6).

Clearance rates (Table 3.5, based on equation (3)) had a mean value of 1.28 l/d at 50 prey/litre and 1.41 l/d at 100 prey/litre; this difference was not statistically significant ($p > 0.05$, Fig.3.7b). Clearance rate at each density was compared with clearance rate at the same density under normal lighting conditions (Fig.3.7b). Whilst there was no significant difference at 50 prey/litre ($p > 0.05$), a statistically significant difference did exist at 100 prey/litre (Fig.3.7b, $p > 0.001$). At higher prey density, foraging therefore appeared to be more effective in the dark.

Table 3.6 Mysid predation on E.affinis in the absence of light

Prey Density	Vessel volume(l)	Mysid length(mm)	No. prey recovered	Control recovery	No. prey taken	No. dead
50	1	14.0	9	(50,50)	41	0
		15.0	13		37	0
		13.5	29		21	0
		13.0	14		36	0
		13.5	11		39	0
100	1	14.5	30	(98,99)	70	0
		15.0	26		74	0
		13.5	17		83	0
		13.0	23		77	0
		14.5	27		73	0

Table 3.7 Mysid predation on E.affinis in the presence of < 69 um naturally-occurring detrital material

Prey Density	Vessel volume(l)	Mysid length(mm)	No. prey recovered	Control recovery	No. prey taken	No. dead
25	2	17.0	28	(50,50)	22	0
		16.5	32		18	0
		15.5	35		15	0
		15.0	28		22	0
		16.0	31		19	0
50	1	13.5	23	(50,50)	27	0
		15.5	17		33	0
		13.0	29		21	0
		14.5	26		24	0
		16.0	24		26	0
100	1	16.0	46	(100,100)	54	0
		14.5	59		41	0
		15.0	46		54	0
		16.5	54		46	0
		15.5	51		49	0

Discussion

Discussion

Field survey

Equipment performance

The sampling equipment performed reliably throughout the survey period, and proved to be an effective method of sampling zooplankton in shallow and turbid waters. No physical damage was incurred by animals present in samples, but passage through the pump did detach eggs sacs from species such as Eurytemora. A field assessment of fecundity in this species was therefore not possible.

Taxa identified

A total of 55 taxa were found in the samples collected, although some of these were identified only to family or higher level. This contrasts with the 135 taxa identified in a contemporary study of the main channel Forth zooplankton by Taylor (1984, 1987). Taylor encountered euphausiids, ctenophores, mysids and a considerably greater variety of meroplanktonic larvae than were found in the littoral/intertidal zone. His samples were, however, numerically dominated by the same restricted group of neritic copepods (Acartia, Oithona, Centropages, Temora, Pseudocalanus) as were the samples in the present survey. A feature of the

present study was the persistent presence and numerical dominance of Eurytemora at all stations throughout much of the year. This species, although showing a seasonal and spatial pattern similar to that reported by Taylor (1984,1987) appears, as observed by Roddie (1980) and dePauw (1973), to concentrate in the margins of estuaries.

The use of a 69 um mesh net in the present study permitted the observation and enumeration of groups such as the small cyclopid Oithona, rotifers, copepod nauplii and cirripede nauplii which are frequently missed in zooplankton surveys. Amongst the meroplanktonic larvae, cirripede nauplii were abundant throughout much of the estuary and most of the year. The other, holoplanktonic, groups, were also widespread and abundant, and would clearly contribute much to seasonal estimates of biomass and production.

Rotifers are rarely reported in zooplankton surveys by virtue of their small size; Synchaeta, the genus dominant in the upper Forth, would not be retained by a mesh of greater than 100 um. Hulsizer (1976) and Allan et al (1976) noted high rotifer abundance during February and March in Chesapeake Bay estuaries, which corresponds to the present findings. These authors also found, however, that this peak coincided with the maximum abundance of Eurytemora; in the present study, the Eurytemora peak succeeded the rotifer peak.

The extension of the survey area upstream of the range covered by Taylor (1984) enables the interface between freshwater and

estuarine communities to be more clearly reflected, and the seasonal, tidal and spatial variation in freshwater influence was readily apparent from the survey results. Peak abundance of Daphnia, Bosmina, and Diaptomus at all upper-estuary stations occurred in January and February 1982, just after the rotifer peak and just before a peak in abundance of Maranzelleria larvae. There was thus a succession of abundance maxima;

Rotifera > freshwater sp. > Maranzelleria > Eurytemora

at Fallin, S.Alloa, Dunmore and Kincardine. Hulsizer (1976) reported a similar succession of rotifers and cladocera in Chesapeake Bay. In contrast, an additional freshwater taxon, chydorid cladocera, achieved maximum abundance and most frequent occurrence in late summer and autumn. This pattern appears to be typical of chydorids (Whiteside, 1974).

The winter peak of rotifers coincided with a winter minimum of Eurytemora. Synchaeta has similar linear dimensions to Eurytemora nauplii, but can, by reproducing parthenogenetically and at a small size, maintain a higher intrinsic population growth rate at low temperatures than can Eurytemora. Competition between nauplii and rotifers for resources may exacerbate the effects of low temperatures on Eurytemora population growth. Conversely, it may be that rotifers can only compete successfully for resources at low Eurytemora abundances, although this might imply a second peak in rotifer numbers during the summer decline in Eurytemora. Williamson and Butler (1986) have demonstrated that Diaptomus can

feed effectively on small rotifers, and it is further possible that the succession of rotifers and Eurytemora is a consequence of predatory interaction.

Amongst the meroplankton, Littorina egg capsules were, as previously shown by Alifierakis and Berry(1980) and Roddie (1980), clearly associated in abundance with high spring tides.

Although not numerically reported, the presence on occasion of large numbers of turbellaria in S.Alloa samples is worthy of note, as these animals may exert significant predation pressure on zooplankton (Maly et al 1980).

Community structure and environmental variables

The zooplankton data were rather sparse, with low abundances and infrequent occurrences of the majority of taxa. With the exception of Eurytemora and the rotifers, Taylor (1984) found higher abundances of most taxa common to both studies. This contrasts with the pilot intertidal study of Roddie (1980) which found generally higher abundances of most taxa than in the present study. Further, since not all samples planned could be taken, the distribution of samples among attributes (tide, station, date) was unbalanced.

Despite these shortcomings, the methods applied in analysis were reasonably successful in describing community structure and its relationship with environmental variables.

Chi-squared test of association between occurrence and sample type

This approach proved reasonably effective in discriminating between species and sample categories. A strong distinction was apparent between the neritic copepod community and marine incursors, and the freshwater community. The relationship between these groups and tidal and spatial variation was also clear.

The larvae of benthic invertebrates were associated with high spring tides (where any association existed), and their occurrence was biased toward lower-estuary stations. This is a reflection of both the location of the parent populations and of the advantages in larval dispersion derived from release during periods of maximum tidal excursion. Greater tidal penetration on spring tides is also likely to account for the higher relative frequency of occurrence of neritic copepods and marine species during this phase of the semilunar cycle.

Classification

Classification analysis indicated that Centropages was confined to spring/summer samples, and was closely allied with the occurrence of terebellid larvae. Oithona and Pseudocalanus were most abundant in spring, but occurred frequently throughout the summer and autumn, and Temora was associated with these species although occurring less frequently. Taylor (1984,1987) found these copepod species generally most abundant in winter.

The seasonal pattern of the Acartia spp. matched that found by Taylor (1984,1987); A.bifilosa inermis and A.longiremis were most abundant in spring and autumn, while A.tonsa had a late summer peak. Polydora and cirripede cyprids occurred primarily in spring but, as noted above, cirripede nauplii were present in many samples throughout the year. The nauplii and cyprids were not distinguished in the samples, but are likely to have been predominantly Balanus in the spring and Elminius during the summer.

In general, the neritic and meroplanktonic assemblages were seen to be associated with higher temperatures and primary production. TS/MDA analysis indicated that Pseudocalanus and Oithona were more persistent than Temora and Centropages; the former pair were common in samples associated with lower salinity and higher freshwater discharge (e.g. in the Skinflats data set). It was evident that primary production increased as a discriminating factor with decreasing distance from the upper tidal limit. This was related to the joint advection of lower

estuary phytoplankton and zooplankton assemblages. Classification also revealed the increasing importance of the freshwater community in the same direction. The species associations were preserved, however, wherever overlap between stations occurred.

Analysis by date group emphasised the importance of seasonal factors, with groups in the latter part of the year reflecting greater positive influence of primary production and temperature. The impact of benthic larval production was exaggerated within date groups 4 and 7.

Analysis of samples grouped by tide indicated that information on structure was preserved in larger, more diverse sample sets. The Oithona/cirripede nauplii/Pseudocalanus association proved to be a robust diagnostic feature of sample division. Salinity was relatively more important for the spring and neap tide categories than for high and low tide categories due to the inclusion of semidiurnal tidal variation in the latter.

For completeness, TS/MDA was conducted on the entire data set. Whilst it was impracticable to represent the results as a two-way table and dendrogram, the vector plot was constructed to illustrate the overall relationship between variables (Fig.4.1). The plot emphasises the overall dominance of salinity, and shows the strong association between salinity and distance from upper tidal limit. Percent organic and tidal state are also clearly linked to salinity, although purely for reasons of definition in

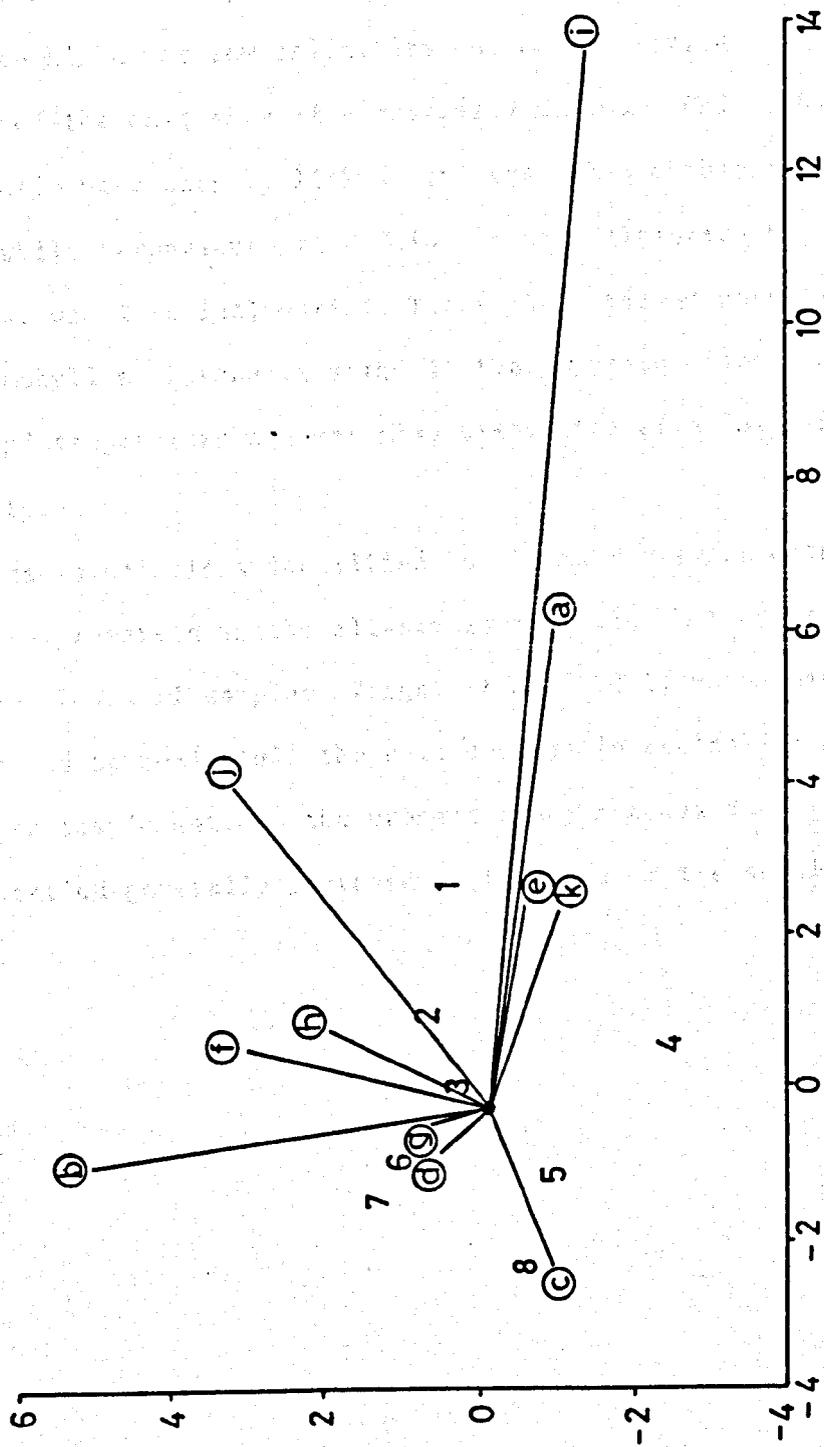


Figure 4.1 Ts/MDA - all samples

Vector plot for all samples combined, showing the location of the centroids of 8 Twinspan groups ordinated in discriminant space on the basis of sample environmental attributes

the latter case.

Date (association with sample cycle) is, as noted previously, approximately orthogonal to salinity and is the second most important variable. Inorganic suspended solids and phaeopigments tended to be higher at low salinities and up-estuary, a reflection of the existence of a turbidity maximum. Chlorophyll a and acid ratio were closely linked, and were also orthogonal to salinity, while temperature tended in the same direction as salinity but was less influential. Temperature showed some link with chlorophyll a. Discharge acted in the opposite direction to salinity and temperature and was also associated with low primary productivity.

The species associations identified in the analysis of data subsets were preserved in the all-sample analysis. MDA correctly reclassified 70.3% of samples. Wright et al (1984), using similar methods, found approximately the same success in reclassification for a larger sample set. In the present study success in reclassification generally improved as the size of the sample set decreased.

Assessment of methods

Whilst DCA ordination followed by correlation with environmental variables demonstrated influence as well as TS/MDA, it was difficult to quantitatively relate the results to community structure since the information about species is not accessible in the final ordination.. This constraint also applies to other ordination methods such as non-metric multidimensional scaling as well as to classification methods based on similarity indices. The Bray-Curtis classifications carried out in the present study were much less intelligible than the TS classifications and have therefore not been reported. A major advantage of TS is that the end-product is a two-way ordered table in which both species and samples are classified. Thus, not only can association between species and sample clusters be identified, but the degree of order in the table can be interpreted as an indicator of the success of the analysis (or of the degree of underlying order).

In the present work, it was possible to independently assess the sensitivity of the analysis since the association of samples belonging to the same logical categories was readily apparent in the dendrogram derived from the table; i.e. within each TS group it was relatively easy to see if samples were grouped on the basis of station, tide or date. Further analysis was, strictly, only necessary where a heterogeneous association of samples within a group was observed.

The utility of MDA has long been recognised in disciplines such as numerical taxonomy and sociology, and Wright et al (1984) and Green and Vascotto (1978) inter alia have demonstrated its application in ecology. By adopting a simple method of variable visualisation, the present study has achieved two things.

Firstly, the relative influence of environmental, spatial and temporal variables in distinguishing between biological groups can readily be demonstrated. Secondly, the overall relationships between variables can be concisely summarised.

The method appears to be robust, in that useful and intelligible information was recovered from an unbalanced and rather 'noisy' data set. In fact, most of the information seemed to be preserved if the data were treated in terms of presence and absence.

Beyond this, semi-quantitative data was sufficient to reflect the influence of seasonal fluctuations in abundance of taxa such as Eurytemora, rotifers and meroplanktonic larvae.

Although Green (1974) described a more rigorous approach to the use of MDA in analysing survey data with temporally-varying environmental data, the present methods were reasonably effective in simultaneously distinguishing the effects of spatial and temporal variables.

Patchiness

1. Dunmore samples: temporal variation at a single site

The back-transformed 95% confidence limits for a single sample were 29-347% ,within the range reported by Gagnon and Lacroix (1981) for a variety of taxa, and are similar to those reported by Roddie et al (1984) from a previous study on the Forth. The uncertainty of an estimate appears to increase with abundance (Gagnon and Lacroix 1981), so abundance estimates based on a single sample need to be treated with caution.

2. Skinflats samples: spatial variation

The patch sizes defined in this work suggest that the routine practice of traversing approximately 100m in sampling still water should have ensured a reasonably representative sample. The maximum range of variation for a single taxon (about a factor of 11 for Eurytemora) was similar to that found at Dunmore. The contrast in distribution about the salinity-temperature front between the copepods and the Polydora larvae is probably a consequence of the distribution of the parent polychaete population; this would, of course, be unrelated to the development of ephemeral high tide water patterns.

The existence of the front is interesting in itself, as an indication of the degree of small-scale heterogeneity in physical characteristics of an estuary.

Eurytemora affinis

The results of field and laboratory investigations on Eurytemora will be considered together in this section.

1. Predation

Whilst clearance rates appeared to be independent of vessel volume at 50 prey/l, there was evidence at 25 prey/l that foraging activity might be relatively constrained in smaller vessels. Thus, mysids in 5 litre vessels appeared to search a larger volume in 24h than those in 2 litre vessels. This contrasts with the findings of Fulton (1982) who reported, in a study of Neomysis and Mysidopsis predation on Acartia and Centropages that clearance rate was independent of vessel volume at all prey densities. In the present study, at 25 prey/l, final prey density was rather similar in both 2 and 5 litre vessels at about 16-18/l. Prey density declined at roughly the same rate in both sizes of vessels; the measured clearance rates may reflect a steady acclimation of effort to declining prey density, and thus point at low prey densities to some inhibition in smaller vessels.

Irrespective of volume, clearance rates were higher at lower prey densities, declining approximately logarithmically as prey density increased. Clearance rates showed evidence of decline at

densities above saturation; this is considered (Fulton 1982, Frost 1975) characteristic of animals displaying a Type II or curvilinear functional response (Holling 1959), although the chi-squared test did not distinguish effectively between the goodness of fit of this model or of a rectilinear model. The curvilinear model yielded an estimate of handling time and maximum daily predation rate of 6.97 min. and about 170/d respectively, while the rectilinear model suggested values of 12 min. and 120/day. Predation rates at up to 100 prey/l were similar to those estimated by Fulton (1982) for Mysidopsis feeding on Acartia. Predator and prey in Fulton's experiments were very similar in size to Neomysis and Eurytemora respectively. Cooper and Goldman (1980), however, reported predation rates of 15mm Mysis relicta which were approximately 50% higher than those reported here.

Visual predation did not appear to be important in Neomysis: indeed, predation rates at higher prey densities were higher in the dark than in the light, which might suggest that the level of illumination interfered with mysid behaviour or perception. Cooper and Goldman (1982) found no difference between foraging rates of Mysis relicta in the light and dark, while Ramcharan and Sprules (1986) found that Mysis relicta had significantly higher predation rates on Daphnia in the light. The high turbidity characteristic of the Neomysis/Eurytemora habitat would, especially in the shallow regions where both species tend to aggregate, render visual predation ineffective much of the time. The omnivorous, nonselective nature of Neomysis foraging was

illustrated by the lack of effect of detritus on predation rate, despite the evidence of ingestion of detritus. A rectilinear model of foraging may, in the light of this, be more appropriate, as it implies a random search pattern and the ingestion of food items in proportion to their abundance.

Neomysis could not be quantitatively sampled in the present study but could, even at a density of $5/m^{-3}$, account for a considerable proportion of the Eurytemora population during the late summer. The potential impact on naupliar and early copepodite stages was not investigated, but could constitute an additional pressure on recruitment success (eg Fig. 4.2).

2. Development rates

Development rate in Eurytemora was not affected by differences in food level, but was quantitatively related to temperature. Final body size was not measured, so unfortunately no information was obtained on growth rate. Corkett and McLaren (1970) noted an inverse relationship between size and development rate.

Development was approximately isochronal, in that a straight line could successfully be fitted to the plot of stage against time. Kelin Breteler et al (1982) described isochronal development in four species of North Sea calanoids, and the data of Vuorinen (1982) for E.hirundoides similarly suggest isochronal

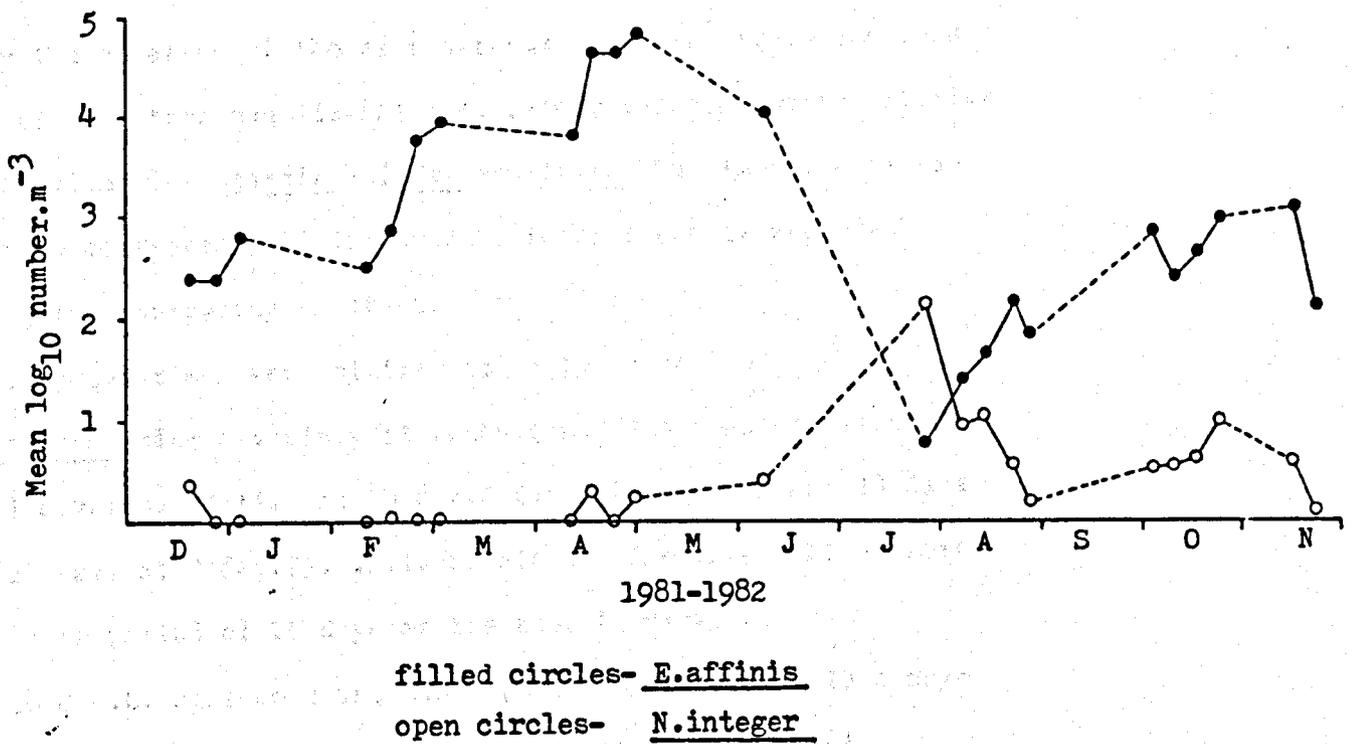


Figure 4.2 Mean upper-estuary abundances

development. It should be noted, however, that in the present study the duration of the n2 stage was consistently longer than that of the other naupliar stages. Landry (1983) reported similar observations for Acartia and Pseudocalanus. The longer n2 stage may be a consequence of the need to replace energy expended during the nonfeeding n1 stage.

Development times were similar to those determined for Eurytemora using a variety of techniques. Vuorinen estimated total development time at 10 deg.C to be between 27 and 33 days (cf 39 days at 8 deg.C), while Heinle and Flemer (1976) estimated a shorter period of 26 days at the same temperature.

At 20 deg.C, agreement was closer, with estimates of 15.5 days and 13.5 days respectively (cf 15.25 days). Estimates of Vijverberg (1980) at 15 deg.C were 8.3 days for nauplii and 9 to 12 days for copepodites, giving a total of 17.3 to 20.3 days (cf 17.0 at 16 deg.C).

The shape of the curve relating temperature to development rate indicated that the effects of temperature were most marked at lower temperatures. Little reduction was apparent from 16 deg. C to 20 deg.C, and it can be concluded that generation time is relatively independent of temperature above 14 deg.C and is highly dependent below this temperature.

3. Field observations

The annual variation in length followed an unusual pattern, most marked in adult females. Conflicting descriptions of the relationship between body length and temperature have been reported in the literature. A negative relationship for copepods was described by Deevey (1960) and Marshall and Orr (1955), but Evans (1977) described a positive relationship for Pseudocalanus. Evans (1977) also reported a bimodal pattern for Temora, similar to that found for Eurytemora in the present work. He subsequently related length variation in Temora to variations in food quality.

Variation in length in Eurytemora in the Forth led to largest body size in September, at water temperatures similar to that at which the annual length minimum occurred; temperature cannot, therefore, be the controlling factor. The length variation was less evident in earlier stages, which were measured only for 9 dates; the more frequent measurements for adult females confirmed that the peak was real. The subsequent decline in body size was followed by a return to normal winter size. The dramatic increase in length (c. 50%) between August and September argues that generation time was short, as no size overlap was apparent. The clear synchrony of change in size between all stages similarly suggests a short adult life span at all seasons.

This study has demonstrated that development rate is strongly temperature-dependent. Combining the findings on development rate with field observations of the relationship between length and

stage led to the prediction of highest daily length increments in August and September and lowest daily length increments in midwinter. Thus, on the one hand, growth rates are similar between samples of radically different body size growing at similar temperatures and on the other growth rates differ widely between specimens of much more similar size growing at very different temperatures. Clearly, temperature cannot be the factor controlling body size and, as noted above, the lack of overlap between samples suggests rapid development so food should not be limiting.

Eurytemora displayed a clear peak of abundance in May, reaching numbers in excess of 250000 m⁻³. Abundances were considerably lower than found by Roddie (1980) somewhat later in the season, and very much lower than maximum numbers reported for this species elsewhere (Burkill et al 1982, Heinle and Flemer 1976). Taylor (1984,1987) has demonstrated, however, that variations in zooplankton abundance between consecutive years can exceed one order of magnitude.

Following the spring peak, abundance declined to a minimum at the same time as body size reached a maximum. A reduction in fecundity might leave more energy available for somatic growth, if the reduction were not itself a consequence of food limitation. The rapidity with which body size increased makes food limitation an unlikely possibility. Alternatively, increased predation pressure from mysids could lead to selection for increased body size as a refuge from attack, although early stages would still

be vulnerable were they present.

One further, simpler, hypothesis might be that the sudden change in size was due to the replacement of the local population by a larger adjacent population. Measurements were not made of size distributions at other sites to test this hypothesis, but evidence can be adduced that in high spring tide samples in May mean female lengths did not differ significantly between Fallin, S.Alloa and Dunmore. It would be likely that, if morphologically distinct populations existed, evidence of advection would have been apparent at that time. In either case, it is possible that seasonal genetic selection could account for the change in size; Bradley (1978) demonstrated seasonal selection for thermal tolerance characteristics in an American Eurytemora population.

Summary

Application of classification and discriminant analysis to one year's field survey data demonstrated the practicability of objectively relating zooplankton community structure to physical, spatial, and temporal variables. Littoral zooplankton have been shown to have a clear structure which agreed well with that described by other studies on the Forth, and which could successfully be defined in terms of the above variables.

Field and laboratory studies relating to Eurytemora affinis demonstrated:

- a) seasonal variation in abundance and size
- b) a well-defined relationship between temperature and development rate
- c) the capacity for predatory interaction between this species and Neomysis, one of the co-dominants of the low salinity region of the estuary.

References

- Alifierakis N S and Berry A J 1980
Rhythmic egg release in Littorina littorea
J. Zool. Lond. 19 297-307
- Allan J D, Kinsey T G, and James M C 1976
Abundances and production of copepods in the Rhode
River subestuary of Chesapeake Bay
Chesapeake Science 17 86-92
- Astthorsson O S, and Ralph R 1984
Growth and Moulting of Neomysis integer
(Crustacea:Mysidacea)
Mar. Biol. 79 55-62
- Boak A C and Goulder R 1983
Bacterioplankton in the diet of the calanoid copepod
Eurytemora sp. in the Humber estuary
Mar. Biol. 73 139-149
- Boleyn B J 1967
A simple pipette control for isolating planktonic algae
Can. J. Microbiol. 13 1129-1130
- Bottrell H H 1975
Generation time, length of life, instar duration and
frequency of moulting, and their relationship to
temperature in eight species of Cladocera from the
River Thames, Reading
Oecologia 19 129-140
- Bradley B P 1978
Increase in the range of temperature tolerance by
acclimation in the copepod Eurytemora affinis
Biol. Bull. 154 177-187
- Bray J R and Curtis J T 1957
An ordination of the upland forest communities of
Southern Wisconsin
Ecol. Monogr. 27 324-349

- Burkill P H and Kendall T F 1982
 Production of the copepod Eurytemora affinis in the
 Bristol Channel
Mar. Ecol. Prog. Ser. 7 21-31
- Burkill P H, Owens N J P and Mantoura R F C 1982
 Zooplankton processes and the food web at the
 freshwater-brackishwater interface (FBI)
Abstract, Bulletin of the Estuarine and Brackishwater
 Sciences Association no. 32 pp 17-18
- Collins N R and Williams R 1982
 Zooplankton communities in the Bristol Channel and
 Severn estuary
Mar. Ecol. Prog. Ser. 9 1-11
- Cooper S D and Goldman C R 1980
 Opossum shrimp (Mysis relicta) predation on zooplankton
Can. J. Fish. Aquat. Sci. 37 909-919
- Cooper S D and Goldman C R 1982
 Environmental factors affecting predation rates of
Mysis relicta
Can. J. Fish. Aquat. Sci. 39 203-208
- Corkett C J and McLaren I A 1970
 Relationships between development rate of eggs and
 older stages of copepods
J. mar. biol. Ass.U.K. 50 161-168
- Deevey G B 1960
 Relative effects of temperature and food on seasonal
 variations in length of marine copepods in some
 eastern American and western European waters.
Bull. Bingham oceanogr. Coll. 17 54-85
- deJorge and Bouwman 1977
 A simple density separation technique for quantitative
 isolation of meiobenthos, using the colloidal silica
 Ludox TM
Mar. Biol. 42 143-148

DePauw N 1973

On the distribution of Eurytemora affinis in the
Western Scheldt estuary

Verh. Internat. Verein. Limnol. 18 1462-1472

Evans F 1977

Seasonal density and production estimates of the
commoner planktonic copepods of Northumberland
coastal waters

Est. Coastal Mar. Sci. 5 223-241

Forth River Purification Board 1983

Annual Report Edinburgh

Frazer W, Barr D I H, and Smith A A 1968

A hydraulic model study of heat dissipation at
Longannet power station

Proc. Instn. Civ. Engrs. 39 23-44

Frolander H F 1968

Statistical variation in zooplankton numbers
subsampling with the Stempel pipette

J. Water Poll. Cont. Fed. 40 82-88

Frost B W 1972

Effects of size and concentration of food particles on
the feeding behaviour of the marine planktonic copepod

Calanus pacificus

Limnol. Oceanogr. 17 805-814

Frost B W 1975

A threshold feeding behaviour in Calanus pacificus

Limnol. Oceanogr. 20 263-266

Fulton R S 1982

Predatory feeding of two marine mysids

Mar. Biol. 183-191

- Furse M T, Moss D, Wright J F and Armitage D 1984
 The influence of seasonal and taxonomic factors on the ordination and classification of running-water sites in Great Britain and on the prediction of their macro-invertebrate communities
Freshwater Biol. 14 257-280
- Gagnon M and Lacroix G 1982
 Zooplankton sample variability in a tidal estuary: an interpretative model
Limnol. Oceanogr. 26 401-411
- Gauch H C and Whittaker R H 1981
 Hierarchical classification of community data
J. Ecol. 69 537-557
- Green R H 1974
 Multivariate niche analysis with temporally varying environmental factors
Ecology 55 73-83
- Green R H and Vascotto G L 1978
 A method for the analysis of environmental factors controlling patterns of species composition in aquatic communities
Water Research 12 583-590
- Heinle D R 1966
 Production of a calanoid copepod, Acartia tonsa in the Patuxent River estuary
Chesapeake Sci. 7 59-74
- Heinle D R and Flemer D A 1975
 Carbon requirements of a population of the estuarine copepod Eurytemora affinis
Mar. Biol. 31 235-247
- Heinle D R, Harris R P, Ustach J F and Flemer D A 1977
 Detritus as food for copepods
Mar. Biol. 40 341-353

Hill M O 1979

Decorana: A Fortran program for Detrended Correspondence
Analysis and Reciprocal Averaging
Cornell University, Ithaca, NY 52 pp

Hill M O 1979

Twinspan: A Fortran program for arranging multivariate
data in an ordered two-way table by classification of
the individuals and attributes
Cornell University, Ithaca, NY 48 pp

Hulsizer E E 1976

Zooplankton of lower Narragansett Bay
Chesapeake Sci. 17 260-270

Katona S K 1971

The developmental stages of Eurytemora affinis raised in
laboratory cultures, including a comparison with the
larvae of E.americana and E.herdmani
Crustaceana 21 5-19

Klein Breteler C H, Fransz H G and Gonzalez S R 1982

Growth and development of four calanoid copepod species
under experimental and natural conditions
Neth. J. Sea Res. 16 195-207

Lance J 1965

Respiration and osmotic behaviour of the copepod Acartia tonsa
in diluted sea-water
Comp. Biochem. Physiol. 14 155-165

Landry M R 1983

The development of marine calanoid copepods with comment
on the isochronal rule
Limnol. Oceanogr. 28 614-624

Leakey R J G 1983

Osmoregulation, respiration and salinity tolerance of the
estuarine copepod Eurytemora affinis
Unpubl. BSc thesis, University of Stirling, 103 pp

Litchfield J T 1949

A method for rapid graphic solution of time-percent
effect curves

J. Pharm. Exp. Therapy 97 399-408

Maly R J, Schoenholtz S and Arts M T 1980

The influence of flatworm predation on zooplankton
inhabiting small ponds

Hydrobiologia 76 233-240

Marin V, Huntley M E and Frost B W 1986

Measuring feeding rates of pelagic herbivores:
analysis of experimental design and methods

Mar. Biol. 93 49-58

Marshall S M and Orr A P 1955

The biology of a marine copepod Calanus fimarchicus
(Gunnerus)

Oliver and Boyd Edinburgh ppl-118

Miller C B 1983

The zooplankton of estuaries

In Estuaries and enclosed seas ed. B H Ketchum

Elsevier Amsterdam pp 103-149

Morris A W, Mantoura R F C, Bales A J and Howland R J M 1978

Very low salinity regions of estuaries: important
sites for chemical and biological reactions

Nature (london) 274 678-680

Nie 1975

Statistical Package for Social Science

McGraw-Hill New York

Nival S and Nival P 1970

A simple device for the sorting of living planktonic
copepods

Limnol. Oceanogr. 16 977-980

- Overall J E and Klett C J 1972
Applied Multivariate Analysis
McGraw-Hill New York
- Ramcharan C W and Sprules W G 1986
Visual predation in Mysis relicta Loven
Limnol. Oceanogr. 31 414-420
- Ricker W E 1973
Linear regression in fishery research
J. Fish. Res. Bd. Can. 30 409-434
- Roddie B D 1980
Some aspects of estuarine zooplankton
Unpubl BSc thesis, University of Stirling, 125 pp
- Roddie B D, R J G Leakey and Berry A J 1984
Salinity-temperature tolerance and osmoregulation
in Eurytemora affinis (Poppe) (Copepoda: Calanoida)
in relation to its distribution in the zooplankton
of the upper reaches of the Forth estuary
J. Exp. Mar. Biol. Ecol. 79 191-211
- Roddie B D 1986
Statistical analysis for marine survey data
Water Research Centre report no. ER 1260-M
- Steedman H F 1976
Zooplankton fixation and preservation
Unesco Press: Paris
- Strickland J D H and Parsons T R 1972
A practical handbook of seawater analysis
Bull. Fish. Res. Bd. Can. 167 1-311
- Taylor C J L 1984
Studies on the zooplankton of the Forth estuary
MSc thesis, University of Stirling 89pp

Taylor C J L 1987

The zooplankton of the Forth, Scotland
Proc. Royal Soc. Edin. 93B 377-388

Vidal J 1980

Physioecology of Zooplankton. II Effects of
phytoplankton concentration, temperature and body size
on the development and molting rate of Calanus pacificus
and Pseudocalanus sp.
Mar. Biol. 56 135-146

Vijverberg J 1980

Effects of temperature in laboratory studies on
growth and development of Cladocera and Copepoda
from Tjeukemeer, the Netherlands
Freshwater Biol. 10 317-340

Vuorinen I 1982

The effect of temperature on the rates of development
of Eurytemora hirundoides (Nordquist) in laboratory
cultures
Ann. Zool. Fennici 19 129-134

Whiteside M C 1974

Chydorid (Cladocera) ecology: seasonal patterns and
abundance of populations in Elk Lake, Minnesota
Ecology 55 538-550

Williamson C E and Butler N M 1986

Predation on rotifers by the suspension-feeding
calanoid copepod Diaptomus pallidus
Limnol. Oceanogr. 3 393-402

Wishart 1970

CLUSTAN: A Fortran program for cluster analysis

Wright J F, Moss D, Armitage P D and Furse M T 1984

A preliminary classification of running-water sites in
Great Britain based on macro-invertebrate species and the
prediction of community type using environmental data
Freshwater Biol. 14 221-256

Appendix A

Environmental variables

Variables are identified in tables as follows:

Tide	tidal state
Date	decimal month
FW disch	mean monthly freshwater discharge (Cumecs)
Susp.solids	total suspended particulate material (mg/l)
%organic	percent of susp.solids lost on ignition
Chla	Chlorophyll a (ug/l)
Phaeo	Phaeopigments (ug/l)
Sal	salinity (‰)
Temp	temperature (deg.C)

Table A1 Environmental variables : Culross

Tide	Date	FW Disch.	Susp. solids	% org	Chla	Phaeo	Sal	Temp
S	3.37	113.1	50.80	8.30	0.00	6.73	25.8	5.5
N	3.60	113.1	40.30	7.45	0.32	3.04	28.6	9.5
S	3.86	113.1	74.18	21.18	3.95	4.35	26.8	10.5
N	4.07	25.1	39.78	8.18	1.18	4.36	23.6	11.5
S	5.32	22.9	17.80	5.75	1.18	1.49	27.5	15.5
N	5.55	22.9	33.20	7.80	9.35	4.02	27.5	14.5
S	5.77	22.9	122.18	22.50	8.61	12.69	28.7	16.5
N	6.00	22.9	*	*	*	*	26.3	17.5
S	7.25	12.1	77.56	24.32	2.54	2.26	32.6	27.5
S	8.84	24.1	*	*	*	*	27.1	19.0
S	9.20	77.9	48.76	13.60	4.33	3.11	26.6	14.5
N	9.43	77.9	40.60	8.75	2.72	1.03	27.0	14.0
S	9.67	77.9	257.90	45.00	7.36	8.49	29.9	16.5
N	9.90	77.9	30.35	6.90	2.48	4.06	10.6	13.0
S	11.10	135.2	33.15	6.30	2.00	0.33	22.9	11.0
N	11.30	135.2	40.08	7.85	2.20	1.89	23.5	11.0
S	11.53	135.2	185.77	35.70	9.88	12.70	26.6	8.0
N	11.73	135.2	61.20	15.40	1.34	2.40	18.6	6.5
S	12.48	114.3	238.50	32.13	6.68	16.55	22.9	13.5
N	12.74	114.3	51.52	11.50	0.00	2.90	26.1	6.5

Table A2 Environmental variables : Skinflats

Tide	Date	FW Disch	Susp. solids	%org	Chla	Phaeo	Sal	Temp
S	0.35	100.0	*	*	*	*	31.0	7.0
S	1.39	97.2	*	*	*	*	27.0	0.0
N	1.61	97.2	*	*	*	*	15.0	3.5
S	1.87	97.2	*	*	*	*	25.0	3.5
N	2.11	79.4	154.60	25.85	0.00	3.45	21.5	1.5
S	3.37	113.1	56.70	9.40	0.00	2.84	27.4	5.0
N	3.60	113.1	32.20	5.45	0.11	4.08	18.6	8.5
S	3.86	113.1	38.33	11.73	0.75	3.81	27.4	9.5
N	4.07	25.1	29.68	7.63	1.18	2.64	23.6	7.5
S	5.32	22.9	33.80	8.75	1.39	4.08	23.4	21.0
S	5.77	22.9	35.08	7.80	4.41	3.14	29.6	14.5
N	6.00	22.9	*	*	*	*	26.2	25.0
S	9.20	77.9	57.36	14.85	7.68	3.66	27.7	12.5
N	9.43	77.9	34.18	6.23	1.34	3.00	27.8	15.0
N	9.90	77.9	24.55	5.65	3.00	1.79	10.4	12.5
S	11.10	135.2	43.10	6.60	2.97	2.99	18.0	10.0
N	11.30	135.2	53.98	8.00	1.67	2.77	20.3	10.0
S	11.53	135.2	205.27	33.13	7.81	12.74	23.9	7.0
N	11.73	135.2	51.93	10.00	1.91	4.78	15.8	5.5
S	12.48	114.3	170.23	27.37	1.00	20.95	27.6	7.5

Table A3 Environmental variables : Kincardine

Tide	Date	FW Disch	Susp. solids	%org	Chla	Phaeo	Sal	Temp
HS	0.35	100.0	*	*	*	*	31.5	7.0
HN	0.58	100.0	*	*	*	*	30.5	2.0
LN	0.58	100.0	*	*	*	*	23.0	2.5
HS	1.39	97.2	*	*	*	*	25.0	2.5
LS	1.39	97.2	*	*	*	*	18.5	1.5
HN	1.61	97.2	*	*	*	*	11.5	3.0
LN	1.61	97.2	*	*	*	*	12.0	2.5
HS	1.87	97.2	*	*	*	*	23.0	4.0
LS	1.87	97.2	*	*	*	*	15.0	3.0
HN	2.11	79.4	26.80	5.60	0.00	1.79	17.5	5.0
LN	2.11	79.4	28.65	5.85	0.00	2.04	11.0	5.0
HS	3.37	113.1	63.90	10.00	0.00	1.65	18.4	4.5
LS	3.37	113.1	494.40	71.80	0.00	18.70	4.6	3.5
HN	3.60	113.1	12.50	2.90	0.00	1.27	20.2	5.0
LN	3.60	113.1	25.55	5.10	0.53	1.48	15.4	6.5
HS	3.86	113.1	52.23	13.78	0.85	3.78	24.4	9.0
LS	3.86	113.1	140.15	29.95	0.67	11.67	10.4	6.5
HN	4.07	25.1	37.77	8.13	1.18	4.06	15.4	8.0
LN	4.07	25.1	156.65	23.45	2.00	8.93	14.0	9.0
HS	5.32	22.9	22.50	5.15	4.57	1.45	26.7	13.5
LS	5.32	22.9	75.10	14.55	2.63	7.97	9.7	11.0
HN	5.55	22.9	17.10	4.20	2.24	3.18	25.0	13.5
LN	5.55	22.9	394.66	60.33	8.19	21.59	16.3	16.0
HS	5.77	22.9	31.73	6.05	4.74	5.21	29.8	13.5
LS	5.77	22.9	60.83	10.85	2.40	6.31	15.6	14.0
HN	6.00	22.9	*	*	*	*	22.9	15.0
LN	6.00	22.9	*	*	*	*	21.5	16.0
HS	7.25	12.1	104.28	23.08	8.33	5.52	30.5	16.5
LS	8.84	24.1	*	*	*	*	24.9	16.5
HS	9.20	77.9	33.91	8.90	7.01	2.80	29.1	13.5
HN	9.43	77.9	23.20	4.25	2.16	1.58	23.1	13.5
LN	9.43	77.9	70.40	15.30	3.20	4.46	14.4	13.0
HS	9.67	77.9	259.90	48.50	6.94	8.03	30.4	14.0
LS	9.67	77.9	61.20	12.30	3.47	3.25	9.6	15.0
LN	9.90	77.9	34.02	7.68	2.34	0.82	8.2	12.0
HS	11.10	135.2	61.40	11.80	1.74	2.54	24.3	10.5
HN	11.30	135.2	50.03	8.60	1.04	1.82	14.4	9.5
LN	11.30	135.2	92.60	14.07	1.47	8.19	3.4	9.5
HS	11.53	135.2	53.32	9.18	2.80	2.87	24.5	8.5
LS	11.53	135.2	637.97	96.63	21.22	24.19	8.2	7.0
HN	11.73	135.2	37.35	8.43	0.00	1.98	23.6	7.0
LN	11.73	135.2	55.60	12.40	0.00	5.69	10.0	5.5
HS	12.48	114.3	106.77	16.70	0.45	10.46	22.8	7.0
LS	12.48	114.3	462.82	62.29	15.14	21.27	13.6	6.0
HN	12.74	114.3	32.37	7.75	0.80	1.53	23.5	5.5
LN	12.74	114.3	49.12	10.55	1.17	3.62	9.1	4.0

Table A4 Environmental variables : Dunmore

Tide	Date	FW disch	Susp. solids	%org	Chla	Phaeo	Sal	Temp
HS	0.35	100.0	*	*	*	*	28.0	7.0
HN	0.58	100.0	*	*	*	*	24.0	1.0
LN	0.58	100.0	*	*	*	*	14.0	0.5
HS	1.39	97.2	*	*	*	*	22.0	0.0
LS	1.39	97.2	*	*	*	*	10.0	0.0
HN	1.61	97.2	*	*	*	*	4.0	2.0
LN	1.61	97.2	*	*	*	*	2.5	1.5
HS	1.87	97.2	*	*	*	*	14.0	3.5
LS	1.87	97.2	*	*	*	*	2.5	4.0
HN	2.11	79.4	22.60	5.20	0.00	2.44	9.0	4.0
LN	2.11	79.4	38.40	5.80	0.00	0.43	1.5	4.0
HS	3.37	113.1	49.20	7.20	0.00	2.64	11.4	5.0
LS	3.37	113.1	304.20	41.00	0.00	10.20	0.6	4.5
HN	3.60	113.1	26.65	4.40	0.00	1.72	6.8	4.5
LN	3.60	113.1	33.20	5.45	0.21	1.81	6.0	5.5
HS	3.86	113.1	35.53	11.03	1.07	3.27	20.8	8.5
LS	3.86	113.1	319.15	55.55	3.87	17.92	2.0	7.0
HN	4.07	25.1	31.83	7.53	0.85	3.03	20.0	7.5
LN	4.07	25.1	100.15	20.95	1.74	7.89	6.4	8.0
HS	5.32	22.9	27.70	7.95	3.50	3.15	19.2	8.5
LS	5.32	22.9	200.20	36.65	2.31	20.43	4.5	12.0
HN	5.55	22.9	44.13	8.13	2.72	4.06	12.8	15.0
LN	5.55	22.9	20.26	4.46	0.85	2.75	9.5	15.5
HS	5.77	22.9	46.63	9.50	4.21	2.49	28.5	14.5
LS	5.77	22.9	104.33	17.70	4.37	19.96	7.2	14.5
HN	6.00	22.9	*	*	*	*	24.6	15.0
LN	6.00	22.9	*	*	*	*	11.1	16.5
HS	7.25	12.1	853.30	142.40	23.96	41.97	25.1	17.0
HS	8.84	24.1	*	*	*	*	21.7	16.5
HS	9.20	77.9	29.76	7.10	18.69	2.57	17.3	13.0
LS	9.20	77.9	225.71	39.25	15.42	23.69	1.5	12.0
HN	9.43	77.9	36.80	7.55	3.74	2.01	21.2	14.0
LN	9.43	77.9	79.45	14.10	4.24	7.05	3.6	13.5
HS	9.67	77.9	43.65	8.30	3.11	2.90	24.2	14.0
LS	9.67	77.9	143.90	28.50	5.61	6.95	4.3	15.0
HN	9.90	77.9	20.40	3.95	3.24	2.56	4.2	11.5
LN	9.90	77.9	284.75	41.95	7.08	19.18	5.4	11.0
HS	11.10	135.2	53.35	8.05	1.17	5.02	11.5	9.5
LS	11.10	135.2	190.95	30.45	1.67	16.55	0.5	9.0
HN	11.30	135.2	56.98	7.75	2.94	6.57	14.5	10.0
LN	11.30	135.2	96.13	13.00	5.52	4.69	2.6	9.0
HS	11.53	135.2	57.03	12.37	3.60	3.31	15.2	7.0
LN	11.53	135.2	383.97	56.43	17.49	17.27	1.8	6.0
HN	11.73	135.2	60.60	13.53	0.98	4.00	3.8	6.5
LN	11.73	135.2	588.80	80.53	12.03	16.72	1.4	5.5
HS	12.48	114.3	86.96	15.10	0.66	7.32	20.6	7.5
LS	12.48	114.3	503.93	83.60	17.81	18.33	4.0	5.0
HN	12.74	114.3	21.36	4.80	0.33	1.54	8.0	2.0
LN	12.74	114.3	10.86	1.95	0.50	0.90	1.9	1.5

Table A5 Environmental variables : S.Alloa

Tide	Date	FW disch	Susp. solids	Xorg	Chla	Phaeo	Sal	Temp
HS	0.35	100.0	*	*	*	*	18.0	7.0
HN	0.58	100.0	*	*	*	*	22.5	0.5
LN	0.58	100.0	*	*	*	*	5.5	0.0
HS	1.39	97.2	*	*	*	*	16.5	0.0
LS	1.39	97.2	*	*	*	*	3.5	0.0
HN	1.61	97.2	*	*	*	*	3.0	2.0
LN	1.61	97.2	*	*	*	*	0.5	1.0
HS	1.87	97.2	*	*	*	*	6.0	3.0
LS	1.87	97.2	*	*	*	*	1.5	3.0
HN	2.11	79.4	15.40	3.95	0.10	0.87	3.5	4.5
LN	2.11	79.4	73.45	10.35	0.00	1.51	0.5	4.0
HS	3.37	113.1	314.70	43.50	0.26	3.04	4.4	5.0
LS	3.37	113.1	267.80	28.70	0.80	7.04	0.0	4.0
HN	3.60	113.1	34.45	6.30	0.00	3.06	2.6	4.5
LN	3.60	113.1	38.15	6.05	0.42	2.64	0.6	5.5
HS	3.86	113.1	37.23	8.78	1.18	3.76	12.2	8.0
LS	3.86	113.1	282.35	49.45	2.14	21.04	0.8	7.0
HN	4.07	25.1	88.95	16.45	1.34	6.78	11.6	7.5
LN	4.07	25.1	237.75	35.45	4.41	9.71	1.0	8.0
HS	5.32	22.9	36.10	9.05	4.27	4.42	12.1	12.5
LS	5.32	22.9	202.70	35.45	2.31	23.95	2.4	11.0
HN	5.55	22.9	16.66	4.26	2.06	2.15	12.6	14.5
LN	5.55	22.9	51.73	9.13	2.19	3.75	1.6	15.0
HS	5.77	22.9	85.93	16.60	2.94	7.18	22.6	14.0
LS	5.77	22.9	266.35	40.20	7.78	18.16	3.5	14.5
HN	6.00	22.9	*	*	*	*	20.0	16.5
LN	6.00	22.9	*	*	*	*	3.2	17.0
HS	7.25	12.1	42.72	11.08	10.95	0.45	19.0	18.0
HS	8.84	24.1	*	*	*	*	17.2	15.5
HS	9.20	77.9	92.51	19.90	8.51	9.95	9.8	11.0
LS	9.20	77.9	465.21	77.95	13.82	42.77	1.0	11.0
HN	9.43	77.9	25.50	4.15	4.67	2.34	10.4	13.5
LN	9.43	77.9	122.65	19.10	4.76	5.08	0.9	13.5
HS	9.67	77.9	77.23	14.40	2.55	2.12	15.9	14.0
LS	9.67	77.9	461.50	70.10	14.77	21.38	1.1	14.5
HN	9.90	77.9	30.40	5.39	4.20	2.15	2.0	11.0
LN	9.90	77.9	338.15	48.35	2.60	13.42	0.8	10.5
HS	11.10	135.2	50.30	7.59	3.10	5.00	6.4	9.5
LS	11.10	135.2	278.35	41.45	8.48	13.81	0.0	9.0
HN	11.30	135.2	59.63	8.50	4.17	3.66	2.6	9.5
LN	11.30	135.2	113.40	17.13	4.32	6.96	0.0	8.5
HS	11.53	135.2	63.50	10.03	4.67	7.94	4.3	6.0
LS	11.53	135.2	349.57	51.63	14.02	18.04	0.2	5.5
HN	11.73	135.2	33.67	7.33	1.02	3.65	2.5	6.0
LN	11.73	135.2	118.00	19.13	4.14	5.74	0.0	5.0
HS	12.48	114.3	217.16	31.30	6.23	6.23	7.7	7.5
LS	12.48	114.3	372.64	52.80	13.19	12.78	0.5	5.0
HN	12.74	114.3	20.12	4.95	0.33	1.89	6.1	2.0
LN	12.74	114.3	26.27	4.80	1.84	1.08	0.0	1.5

Table A6 Environmental variables : Fallin

Tide	Date	FW disch	Susp. solids	%org	Chla	Phaeo	Sal	Temp
HS	0.35	100.0	*	*	*	*	11.0	7.0
HN	0.58	100.0	*	*	*	*	5.0	0.0
LN	0.58	100.0	*	*	*	*	0.5	0.0
HS	1.39	97.2	*	*	*	*	5.0	0.0
LS	1.39	97.2	*	*	*	*	0.5	0.0
HN	1.61	97.2	*	*	*	*	0.5	1.0
LN	1.61	97.2	*	*	*	*	0.0	1.0
HS	1.87	97.2	*	*	*	*	0.0	2.5
LS	1.87	97.2	*	*	*	*	0.0	2.5
HN	2.11	79.4	15.300	2.55	0.00	0.90	0.0	4.5
LN	2.11	79.4	92.450	10.20	0.00	2.32	0.0	3.5
HS	3.37	113.1	215.500	22.60	0.00	3.74	0.2	4.5
LS	3.37	113.1	95.800	10.80	0.00	3.74	0.0	4.0
HN	3.60	113.1	9.000	1.45	1.28	0.81	0.2	5.0
LN	3.60	113.1	14.600	2.45	0.96	0.31	0.0	5.0
HS	3.86	113.1	167.500	30.75	3.38	12.94	2.2	7.5
LS	3.86	113.1	264.250	41.75	1.87	14.02	0.2	6.5
HN	4.07	25.1	83.250	13.85	1.82	6.48	1.4	7.0
LN	4.07	25.1	4.065	7.55	0.69	3.44	0.1	7.5
HS	5.32	22.9	74.700	16.20	2.90	22.39	3.5	11.0
LS	5.32	22.9	249.500	47.75	5.34	18.02	0.8	11.0
HN	5.55	22.9	50.900	8.46	3.31	3.49	1.3	14.5
LN	5.55	22.9	22.460	4.46	4.67	2.70	0.2	14.5
HS	5.77	22.9	238.950	32.90	2.49	15.08	12.2	14.5
LS	5.77	22.9	173.950	28.30	11.39	16.92	0.0	14.5
HN	6.00	22.9	*	*	*	*	6.5	16.5
LN	6.00	22.9	*	*	*	*	0.8	17.0
HS	7.25	12.1	62.480	13.88	33.51	1.70	5.7	19.0
HS	8.84	24.1	*	*	*	*	0.2	15.0
HS	9.20	77.9	109.710	29.55	15.35	38.38	2.6	10.0
LS	9.20	77.9	458.110	66.55	8.89	24.06	0.2	10.5
HN	9.43	77.9	77.050	8.90	2.14	4.41	1.5	13.0
LN	9.43	77.9	86.850	12.83	2.50	3.45	0.2	13.0
LS	9.67	77.9	375.200	61.10	11.99	16.07	0.0	14.0
HN	9.90	77.9	42.200	5.75	3.00	2.49	0.2	12.0
LN	9.90	77.9	648.950	91.75	17.11	44.22	0.1	11.0
HS	11.10	135.2	368.950	49.45	9.35	12.38	0.0	9.5
LS	11.10	135.2	90.450	9.68	2.89	4.89	0.0	9.0
HN	11.30	135.2	31.330	3.05	1.57	2.15	0.0	9.0
LN	11.30	135.2	25.270	3.80	2.32	0.80	0.0	8.5
HS	11.53	135.2	136.970	17.30	4.14	6.14	0.0	5.5
HN	12.74	114.3	19.410	2.60	0.33	1.89	0.4	2.0
LN	12.74	114.3	16.400	3.00	1.34	0.65	0.0	2.0

Appendix B: Zooplankton abundances

Table Bl a: Fallin

STATION	ETEOLARV	NERELARV	MARAWIRE	MARAEGGS	MARATROC	BIVALARV
F11.12HS	0	0	0	0	0	0
F18.12HN	0	0	0	0	0	0
F18.12LN	0	0	0	0	0	0
F12.01HS	0	0	0	0	0	0
F12.01LS	0	0	0	0	0	0
F19.01HN	0	0	0	0	0	0
F19.01LN	0	0	0	0	0	0
F27.01HS	0	0	0	0	0	0
F27.01LS	0	0	0	0	0	0
F03.02HN	0	0	0	0	0	0
F03.02LN	0	0	0	0	0	0
F11.03HS	0	0	4	0	0	0
F11.03LS	0	0	0	0	0	0
F17.03HN	0	0	141	17	0	0
F17.03LN	0	0	4	0	0	0
F26.03HS	0	0	142	4	0	0
F26.03LS	0	0	2	0	0	0
F02.04HN	0	0	321	0	0	0
F02.04LN	0	0	0	0	0	0
F10.05HS	0	104	0	0	0	0
F10.05LS	0	2	12	0	0	0
F17.05HN	0	0	0	0	0	0
F17.05LN	0	0	0	0	0	0
F24.05HS	0	9	0	0	0	0
F24.05LS	0	0	0	0	0	0
F31.05HN	0	0	0	0	0	0
F31.05LN	0	0	0	0	0	0
F08.07HS	0	0	0	0	0	0
F26.08HS	0	0	0	0	0	0
F06.09HS	0	0	0	0	0	0
F06.09LS	0	0	0	0	0	0
F13.09HN	0	0	0	0	0	0
F13.09LN	0	0	0	0	0	0
F20.09LS	0	0	0	0	0	0
F27.09HN	0	0	0	0	0	0
F27.09LN	0	0	0	0	0	0
F03.11HS	0	0	0	0	0	0
F03.11LS	0	0	0	0	0	0
F09.11HN	0	0	0	0	0	0
F09.11LN	0	0	0	0	0	0
F16.11LS	0	0	0	0	0	0
F23.12HN	0	0	0	0	0	0
F23.12LN	0	0	0	0	0	0

Table B1 b: Fallin

STATION	LITTCAPS	LITVELI	CIRRNAUP	CIRRCYPR	TERELARV	POLYCILI
F11.12HS	0	0	0	0	0	0
F18.12HN	58	0	0	0	0	0
F18.12LN	0	0	0	0	0	0
F12.01HS	0	0	0	9	0	0
F12.01LS	0	0	0	4	0	0
F19.01HN	0	0	0	0	0	0
F19.01LN	0	0	0	0	0	0
F27.01HS	0	0	0	0	0	0
F27.01LS	0	0	0	0	0	0
F03.02HN	0	0	0	0	0	0
F03.02LN	0	0	0	0	0	0
F11.03HS	27	0	2	0	0	0
F11.03LS	0	0	0	0	0	0
F17.03HN	2	0	2	0	0	0
F17.03LN	0	0	0	0	0	0
F26.03HS	5	5	4	0	0	0
F26.03LS	0	0	0	0	0	0
F02.04HN	0	0	0	0	0	0
F02.04LN	1	0	0	0	0	0
F10.05HS	0	0	0	0	0	0
F10.05LS	0	0	0	0	0	0
F17.05HN	2	0	0	0	0	0
F17.05LN	0	0	0	0	0	0
F24.05HS	0	0	0	0	0	17
F24.05LS	0	0	0	0	0	4
F31.05HN	0	0	0	0	0	0
F31.05LN	0	0	0	0	0	2
F08.07HS	0	0	0	0	0	0
F26.08HS	0	0	0	0	0	2
F06.09HS	0	0	0	0	0	4
F06.09LS	0	0	0	0	0	0
F13.09HN	0	0	0	0	0	0
F13.09LN	0	0	0	0	0	0
F20.09LS	0	0	0	0	0	0
F27.09HN	0	0	0	0	0	0
F27.09LN	2	0	0	0	0	0
F03.11HS	0	0	0	0	0	0
F03.11LS	0	0	0	0	0	0
F09.11HN	0	0	0	0	0	0
F09.11LN	0	0	0	0	0	0
F16.11LS	0	0	0	0	0	0
F23.12HN	0	0	0	0	0	0
F23.12LN	0	0	0	0	0	0

Table B1 c: Fallin

STATION	PSEUELON	TEMOLONG	CENTHAMA	CALAHELG	SAGIELEG	OIKODIOI
F11.12HS	0	0	0	0	0	0
F18.12HN	0	0	0	0	0	0
F18.12LN	0	0	0	0	0	0
F12.01HS	0	0	0	0	0	0
F12.01LS	0	0	0	0	0	0
F19.01HN	0	0	0	0	0	0
F19.01LN	0	0	0	0	0	0
F27.01HS	0	0	0	0	0	0
F27.01LS	0	0	0	0	0	0
F03.02HN	0	0	0	0	0	0
F03.02LN	0	0	0	0	0	0
F11.03HS	0	0	0	0	0	0
F11.03LS	0	0	0	0	0	0
F17.03HN	0	0	0	0	0	0
F17.03LN	0	0	0	0	0	0
F26.03HS	0	0	0	0	0	0
F26.03LS	0	0	0	0	0	0
F02.04HN	0	0	0	0	0	0
F02.04LN	0	0	0	0	0	0
F10.05HS	0	0	0	0	0	0
F10.05LS	0	0	0	0	0	0
F17.05HN	0	0	0	0	0	0
F17.05LN	0	0	0	0	0	0
F24.05HS	0	0	0	0	0	0
F24.05LS	0	0	0	0	0	0
F31.05HN	0	0	0	0	0	0
F31.05LN	0	0	0	0	0	0
F08.07HS	0	0	0	0	0	0
F26.08HS	0	0	0	0	0	0
F06.09HS	2	0	0	0	0	0
F06.09LS	0	0	0	0	0	0
F13.09HN	0	0	0	0	0	0
F13.09LN	0	0	0	0	0	0
F20.09LS	0	0	0	0	0	0
F27.09HN	0	0	0	0	0	0
F27.09LN	0	0	0	0	0	0
F03.11HS	0	0	0	0	0	0
F03.11LS	38	0	0	0	0	0
F09.11HN	0	0	0	0	0	0
F09.11LN	0	0	0	0	0	0
F16.11LS	0	0	0	0	0	0
F23.12HN	0	0	0	0	0	0
F23.12LN	0	0	0	0	0	0

Table B1 d: Fallin

STATION	ACARINER	ACARTONS	ACARLONG	ACARCLAU	ACARCOPE	OITHSIMI
F11.12HS	0	0	0	0	0	0
F18.12HN	0	0	0	0	0	0
F18.12LN	0	0	0	0	0	0
F12.01HS	0	0	0	0	0	0
F12.01LS	0	0	0	0	0	0
F19.01HN	0	0	0	0	0	0
F19.01LN	0	0	0	0	0	0
F27.01HS	0	0	0	0	0	0
F27.01LS	0	0	0	0	0	0
F03.02HN	0	0	0	0	0	0
F03.02LN	0	0	0	0	0	0
F11.03HS	0	0	0	0	0	0
F11.03LS	0	0	0	0	0	0
F17.03HN	0	0	0	0	0	0
F17.03LN	0	0	0	0	0	0
F26.03HS	0	0	0	0	0	0
F26.03LS	0	0	0	0	0	0
F02.04HN	0	0	0	0	0	0
F02.04LN	0	0	0	0	0	0
F10.05HS	0	0	0	0	0	0
F10.05LS	0	0	0	0	0	0
F17.05HN	0	0	0	0	0	0
F17.05LN	0	0	0	0	0	0
F24.05HS	0	0	0	0	17	0
F24.05LS	0	0	0	0	0	0
F31.05HN	0	0	0	0	0	0
F31.05LN	0	0	0	0	0	0
F08.07HS	0	0	24	0	0	0
F26.08HS	0	0	0	0	0	0
F06.09HS	2	0	9	0	0	0
F06.09LS	0	0	0	0	0	0
F13.09HN	0	0	0	0	0	0
F13.09LN	0	0	0	0	0	0
F20.09LS	0	0	0	0	0	0
F27.09HN	0	0	0	0	0	0
F27.09LN	0	2	0	0	0	0
F03.11HS	0	0	0	0	0	3
F03.11LS	8	0	0	0	4	0
F09.11HN	0	0	0	0	0	0
F09.11LN	0	0	0	0	0	0
F16.11LS	0	0	0	0	0	0
F23.12HN	0	0	0	0	0	0
F23.12LN	0	0	0	0	0	0

Table B1 f: Fallin

STATION	EAFFADUL	EAFFCOPE	EAFFJUVE	HARPSPEC	ROTISPEC	COPENAUP
F11.12HS	776	3771	10117	600	159740	0
F18.12HN	328	245	0	298	57	0
F18.12LN	8	51	232	65	14487	0
F12.01HS	552	597	6144	1179	126633	0
F12.01LS	0	22	92	177	437	0
F19.01HN	0	44	78	25	530	37
F19.01LN	16	8	12	41	53	0
F27.01HS	69	113	4	17	1044	0
F27.01LS	0	0	0	17	165	0
F03.02HN	35	163	528	4	10647	0
F03.02LN	8	0	18	18	169	0
F11.03HS	11	25	23	29	57	43
F11.03LS	0	0	32	0	30	30
F17.03HN	4	43	34	4	39	96
F17.03LN	2	15	71	14	87	48
F26.03HS	1450	6173	19582	277	0	0
F26.03LS	24	74	209	31	14	29
F02.04HN	1348	2538	20392	56	16	112
F02.04LN	38	28	12	18	4	9
F10.05HS	14927	36214	88362	2	2192	0
F10.05LS	309	169	475	90	77	0
F17.05HN	36139	22750	39630	12	0	1232
F17.05LN	38540	20636	712	0	0	0
F24.05HS	14521	98390	153120	56	82560	0
F24.05LS	128	262	5108	19	0	369
F31.05HN	3168	53950	193621	6	91	0
F31.05LN	81275	70317	30968	4	0	0
F08.07HS	9818	4573	11565	43	59	0
F26.08HS	2	0	4	15	0	0
F06.09HS	32	5	34	7	9	63
F06.09LS	0	0	6	6	0	8
F13.09HN	7	2	8	5	11	16
F13.09LN	0	0	11	0	41	20
F20.09LS	0	0	69	22	14	11
F27.09HN	0	26	16	0	9	7
F27.09LN	19	2	2	7	7	9
F03.11HS	68	136	298	17	166	28
F03.11LS	25	12	17	21	25	0
F09.11HN	0	39	32	13	64	32
F09.11LN	4	2	2	0	66	39
F16.11LS	0	84	92	8	46	0
F23.12HN	18	28	6	0	15	4
F23.12LN	0	0	0	0	0	0

Table B2 a:South Alloa

STATION	ETEOLARY	NERELARY	MARAWIRE	MARAEGGS	MARATROC	BIVALARY
S11.12HS	0	0	0	0	0	0
S18.12HN	0	0	0	0	0	0
S18.12LN	0	0	0	0	0	0
S12.01HS	0	0	0	0	0	0
S12.01LS	0	0	0	0	0	0
S19.01HN	0	0	0	0	0	0
S19.01LN	0	0	0	0	0	0
S27.01HS	0	0	0	0	0	0
S27.01LS	0	0	0	0	0	0
S03.02HN	0	0	0	0	0	0
S03.02LN	0	0	0	0	0	0
S11.03HS	0	0	1436	700	150	0
S11.03LS	0	0	9	2	0	0
S17.03HN	0	0	574	0	0	0
S17.03LN	0	0	13	0	0	0
S26.03HS	0	0	3145	396	440	0
S26.03LS	0	0	16	5	0	0
S02.04HN	0	0	57055	0	0	0
S02.04LN	0	0	83	0	0	0
S10.05HS	2	27	0	0	0	0
S10.05LS	0	6	8	0	0	0
S17.05HN	0	0	0	0	0	0
S17.05LN	0	0	12	0	0	0
S24.05HS	0	4	0	0	0	0
S24.05LS	2	17	0	0	0	0
S31.05HN	0	0	0	0	0	0
S31.05LN	0	0	0	0	0	0
S08.07HS	0	0	2	0	0	0
S26.08HS	0	0	0	0	0	0
S06.09HS	0	0	0	0	0	0
S06.09LS	0	0	0	0	0	0
S13.09HN	0	0	0	0	0	0
S13.09LN	0	0	0	0	0	0
S20.09HS	0	0	0	0	0	0
S20.09LS	0	0	0	0	0	0
S27.09HN	0	0	0	0	0	0
S27.09LN	0	0	0	0	0	0
S03.11HS	0	0	0	0	0	0
S03.11LS	0	0	0	0	0	0
S09.11HN	0	0	0	0	0	0
S09.11LN	0	0	0	0	0	0
S16.11HS	0	0	0	0	0	0
S16.11LS	0	0	0	0	0	0
S23.11HN	0	0	0	0	0	0
S23.11LN	0	0	0	0	0	0
S15.12HS	0	0	0	0	0	0
S15.12LS	0	0	0	0	0	0
S23.12HN	0	0	0	0	0	0
S23.12LN	0	0	0	0	0	0

Table B2 b: South Alloa

STATION	LITTCAPS	LITTVELI	CIRRNAUP	CIRRCYPR	TERELARV	POLYCILI
S11.12HS	0	0	0	0	0	0
S18.12HN	0	0	9	0	0	0
S18.12LN	0	0	0	0	0	0
S12.01HS	0	0	4	0	0	0
S12.01LS	0	0	0	0	0	0
S19.01HN	0	0	0	0	0	0
S19.01LN	0	0	0	0	0	0
S27.01HS	0	0	0	0	0	0
S27.01LS	0	0	0	0	0	0
S03.02HN	0	0	0	0	0	0
S03.02LN	27	0	0	0	0	0
S11.03HS	18	0	25	0	0	0
S11.03LS	7	0	0	0	0	0
S17.03HN	0	0	6	0	0	0
S17.03LN	0	0	2	0	0	0
S26.03HS	25	7	7	0	0	0
S26.03LS	0	0	0	0	0	0
S02.04HN	0	11	8	0	4	0
S02.04LN	0	0	0	0	0	0
S10.05HS	0	4	2	4	2	21
S10.05LS	0	0	0	0	0	2
S17.05HN	0	0	2	2	0	36
S17.05LN	0	0	0	6	0	0
S24.05HS	4	4	8	8	8	113
S24.05LS	0	0	0	0	0	86
S31.05HN	0	0	0	16	4	12
S31.05LN	2	0	2	0	0	0
S08.07HS	0	0	0	2	0	9
S26.08HS	0	0	0	0	0	5
S06.09HS	0	0	0	0	0	34
S06.09LS	0	0	0	0	0	0
S13.09HN	0	0	22	0	0	9
S13.09LN	0	0	0	0	0	0
S20.09HS	0	0	0	5	0	0
S20.09LS	0	0	0	10	0	0
S27.09HN	0	0	9	0	0	2
S27.09LN	5	0	0	0	0	0
S03.11HS	0	0	0	0	0	0
S03.11LS	0	0	0	0	0	0
S09.11HN	0	0	0	0	0	0
S09.11LN	0	0	0	0	0	0
S16.11HS	0	0	0	0	0	0
S16.11LS	0	0	0	0	0	0
S23.11HN	0	0	0	0	0	0
S23.11LN	0	0	0	0	0	0
S15.12HS	0	0	0	0	0	0
S15.12LS	0	0	0	0	0	0
S23.12HN	0	0	2	0	0	0
S23.12LN	0	0	0	0	0	0

Table B2 c: South Alloa

STATION	PSEUELON	TEMOLONG	CENTHAMA	CALAHELG	SAGIELEG	DIKODIOI
S11.12HS	0	0	0	0	0	0
S18.12HN	0	9	0	0	0	0
S18.12LN	0	0	0	0	0	0
S12.01HS	0	0	0	0	0	0
S12.01LS	0	0	0	0	0	0
S19.01HN	0	0	0	0	0	0
S19.01LN	0	0	0	0	0	0
S27.01HS	0	0	0	0	0	0
S27.01LS	0	0	0	0	0	0
S03.02HN	0	0	0	0	0	0
S03.02LN	0	0	0	0	0	0
S11.03HS	0	0	0	0	0	0
S11.03LS	0	2	0	0	0	0
S17.03HN	2	11	0	0	0	0
S17.03LN	0	0	0	0	0	0
S26.03HS	0	0	0	0	0	0
S26.03LS	0	0	0	0	0	0
S02.04HN	0	0	0	0	0	0
S02.04LN	0	0	0	0	0	0
S10.05HS	6	8	17	8	0	0
S10.05LS	0	0	0	0	0	0
S17.05HN	0	0	0	0	0	0
S17.05LN	0	0	0	0	0	0
S24.05HS	25	30	100	0	0	0
S24.05LS	0	0	0	0	0	0
S31.05HN	4	0	2	0	0	0
S31.05LN	0	0	0	0	0	0
S08.07HS	0	0	0	0	0	0
S26.08HS	0	0	0	0	0	0
S06.09HS	0	0	0	0	0	0
S06.09LS	0	0	0	0	0	0
S13.09HN	0	0	0	0	0	0
S13.09LN	0	0	0	0	0	0
S20.09HS	0	0	0	0	0	0
S20.09LS	0	0	0	0	0	0
S27.09HN	0	0	0	0	0	0
S27.09LN	0	0	0	0	0	0
S03.11HS	0	0	0	0	0	0
S03.11LS	0	0	0	0	0	0
S09.11HN	2	0	0	0	0	0
S09.11LN	0	0	0	0	0	0
S16.11HS	0	0	0	0	0	0
S16.11LS	0	0	0	0	0	0
S23.11HN	0	0	0	0	0	0
S23.11LN	4	0	0	0	0	0
S15.12HS	0	0	0	0	0	0
S15.12LS	0	0	0	0	0	0
S23.12HN	6	0	0	0	0	0
S23.12LN	0	0	0	0	0	0

Table B2 d: South Alloa

STATION	ACARINER	ACARTONS	ACARLONG	ACARCLAU	ACARCOPE	OITHSIMI
S11.12HS	0	0	0	0	0	13
S18.12HN	0	0	0	0	0	30
S18.12LN	0	0	0	0	0	0
S12.01HS	0	0	0	0	0	0
S12.01LS	0	0	0	0	0	4
S19.01HN	0	0	0	0	0	0
S19.01LN	0	0	0	0	0	0
S27.01HS	4	0	0	0	0	0
S27.01LS	0	0	0	0	0	0
S03.02HN	0	0	0	0	0	0
S03.02LN	0	0	0	0	4	2
S11.03HS	0	0	0	0	0	0
S11.03LS	0	0	0	0	4	2
S17.03HN	2	0	0	0	0	0
S17.03LN	0	0	0	0	0	0
S26.03HS	0	0	0	0	0	0
S26.03LS	0	0	0	0	0	2
S02.04HN	2	0	0	0	0	0
S02.04LN	0	0	0	0	4	2
S10.05HS	0	0	0	0	0	0
S10.05LS	0	0	0	0	0	0
S17.05HN	0	0	0	0	0	0
S17.05LN	0	0	0	0	0	0
S24.05HS	8	0	43	0	82	8
S24.05LS	0	0	0	0	0	0
S31.05HN	0	0	6	0	0	0
S31.05LN	0	0	68	0	29	5
S08.07HS	0	41	0	0	12	0
S26.08HS	0	116	0	0	45	0
S06.09HS	0	0	0	0	0	0
S06.09LS	0	11	0	0	11	2
S13.09HN	0	5	0	0	0	0
S13.09LN	0	86	0	0	6	0
S20.09HS	0	0	0	0	5	0
S20.09LS	0	0	0	0	0	0
S27.09HN	0	0	0	0	0	0
S27.09LN	0	0	0	0	8	0
S03.11HS	0	0	0	0	0	0
S03.11LS	0	0	0	0	0	0
S09.11HN	0	0	0	0	0	0
S09.11LN	0	0	0	0	2	0
S16.11HS	0	0	0	0	0	0
S16.11LS	0	0	0	0	2	0
S23.11HN	0	0	0	0	0	0
S23.11LN	0	0	0	0	0	0
S15.12HS	0	0	0	0	0	0
S15.12LS	0	0	0	0	4	4
S23.12HN	0	0	0	0	0	0
S23.12LN	0	0	0	0	0	0

Table B2 e: South Alloa

STATION	NEOMINTE	DIAPGRAC	DAPHSPEC	BOSMSPEC	CHYDSPEC	CYCLSPEC
S11.12HS	0	0	0	0	0	0
S18.12HN	0	0	0	0	0	0
S18.12LN	0	0	0	0	0	0
S12.01HS	0	0	0	0	0	0
S12.01LS	0	4	0	0	0	0
S19.01HN	12	12	8	0	0	0
S19.01LN	12	53	12	0	0	0
S27.01HS	0	35	0	35	0	0
S27.01LS	0	15	0	29	0	0
S03.02HN	0	9	0	41	0	0
S03.02LN	0	27	0	27	0	0
S11.03HS	0	2	0	0	0	0
S11.03LS	0	11	2	21	0	0
S17.03HN	0	22	13	0	0	0
S17.03LN	2	17	4	0	0	0
S26.03HS	0	0	0	0	0	0
S26.03LS	0	0	0	0	0	0
S02.04HN	0	0	0	0	0	0
S02.04LN	0	2	0	0	0	0
S10.05HS	0	0	0	0	0	0
S10.05LS	0	0	0	0	0	2
S17.05HN	0	0	0	0	0	0
S17.05LN	16	0	0	0	0	0
S24.05HS	0	0	0	0	0	0
S24.05LS	0	0	0	0	0	2
S31.05HN	0	0	0	0	0	0
S31.05LN	0	0	0	0	0	0
S08.07HS	4	4	0	0	0	0
S26.08HS	0	0	0	0	0	0
S06.09HS	0	0	0	0	0	0
S06.09LS	0	215	0	6	53	6
S13.09HN	0	2	0	0	0	0
S13.09LN	883	0	0	0	0	0
S20.09HS	2	0	0	0	0	0
S20.09LS	5	0	0	0	10	10
S27.09HN	0	2	7	2	0	0
S27.09LN	9	0	0	5	0	9
S03.11HS	0	0	0	0	2	0
S03.11LS	4	0	0	0	0	0
S09.11HN	0	0	0	0	0	11
S09.11LN	11	6	0	2	0	0
S16.11HS	0	0	0	0	0	0
S16.11LS	14	2	0	0	0	0
S23.11HN	0	12	6	0	0	0
S23.11LN	16	0	0	0	0	0
S15.12HS	0	0	0	0	0	0
S15.12LS	56	0	0	0	7	0
S23.12HN	0	0	0	0	0	0
S23.12LN	3	12	0	0	0	3

Table B2 f: South Alloa

STATION	EAFFADUL	EAFFCOPE	EAFFJUVE	HARPSPEC	ROTISPEC	COPENAUP
S11.12HS	3428	3298	2143	118	13550	0
S18.12HN	758	3674	523	790	338495	0
S18.12LN	92	365	416	4	241	0
S12.01HS	141	1005	13371	833	94102	0
S12.01LS	53	48	1296	629	37212	0
S19.01HN	78	362	1785	50	23662	0
S19.01LN	16	0	74	45	107	0
S27.01HS	382	1552	2244	47	52435	0
S27.01LS	15	22	224	22	8952	0
S03.02HN	191	3010	10944	95	341250	0
S03.02LN	254	27	318	41	4545	0
S11.03HS	178	556	3242	554	1415	502
S11.03LS	16	27	8	43	32	27
S17.03HN	91	1256	2205	13	21	87
S17.03LN	53	124	286	31	114	164
S26.03HS	150	1694	3141	36	47	293
S26.03LS	20654	18702	15180	45	0	0
S02.04HN	307	3348	10449	51	94	539
S02.04LN	495	600	5775	182	224	0
S10.05HS	121	7333	10229	21	73	1587
S10.05LS	2540	4043	12025	132	0	56
S17.05HN	1971	34852	26564	6	1385	1774
S17.05LN	7228	1491	7889	154	0	430
S24.05HS	7913	33999	7476	78	19217	739
S24.05LS	2739	28759	64782	115	2304	1086
S31.05HN	3209	40168	28909	18	5685	0
S31.05LN	15895	19824	34670	47	0	0
S08.07HS	770	15215	29364	23	8370	8163
S26.08HS	17	7	0	20	0	131
S06.09HS	57	96	46	0	37	572
S06.09LS	6	50	9	68	62	136
S13.09HN	15	9	104	7	42	721
S13.09LN	35	0	0	0	25	16
S20.09HS	129	285	1128	23	144	1822
S20.09LS	0	14	114	53	19	110
S27.09HN	0	63	270	7	12	80
S27.09LN	19	5	14	5	14	9
S03.11HS	382	1782	1132	8	53	31
S03.11LS	8	8	20	71	30	30
S09.11HN	84	183	415	0	567	21
S09.11LN	4	12	15	137	21	38
S16.11HS	348	1781	4950	82	13439	10
S16.11LS	165	30	66	88	62	19
S23.11HN	166	458	2575	0	2016	60
S23.11LN	269	4	8	2	32	0
S15.12HS	71	411	1059	183	6449	10
S15.12LS	1183	115	269	854	228	142
S23.12HN	306	986	914	12	7510	14
S23.12LN	17	6	24	0	58	6

Table B3 a: Dunmore

STATION	ETEOLARV	NERELARV	MARAWIRE	MARAEGGS	MARATROC	BIVALARV
D11.12HS	0	0	0	0	0	0
D18.12HN	0	0	0	0	0	0
D18.12LN	0	0	0	0	0	0
D12.01HS	0	0	4	0	0	0
D12.01LS	0	0	0	0	0	0
D19.01HN	0	0	0	0	0	0
D19.01LN	0	0	0	0	0	0
D27.01HS	0	0	9	0	0	0
D27.01LS	0	0	9	0	0	0
D03.02HN	0	0	0	0	0	0
D03.02LN	0	0	0	0	0	0
D11.03HS	0	0	3383	1120	420	0
D11.03LS	0	0	78	73	0	0
D17.03HN	0	0	3706	0	0	0
D17.03LN	0	0	225	0	0	0
D26.03HS	0	0	5653	1060	860	0
D26.03LS	0	0	973	350	117	0
D02.04HN	0	0	16022	0	0	0
D02.04LN	0	0	2258	0	0	0
D10.05HS	0	68	261	0	0	0
D10.05LS	6	27	20	0	0	0
D17.05HN	0	12	0	0	0	0
D17.05LN	0	0	0	0	0	0
D24.05HS	4	43	0	0	0	0
D24.05LS	13	6	0	0	0	8
D31.05HN	0	30	0	0	0	4
D31.05LN	0	0	0	0	0	0
D08.07HS	0	4	0	0	0	0
D26.08HS	0	0	0	0	0	0
D06.09HS	0	0	0	0	0	0
D06.09LS	0	0	0	0	0	0
D13.09HN	0	0	0	0	0	0
D13.09LN	0	0	0	0	0	0
D20.09HS	0	0	0	0	0	0
D20.09LS	0	0	0	0	0	0
D27.09HN	0	0	0	0	0	0
D27.09LN	0	0	0	0	0	0
D03.11HS	0	0	0	0	0	0
D03.11LS	0	0	0	0	0	0
D09.11HN	0	0	0	0	0	0
D09.11LN	0	0	0	0	0	0
D16.11HS	0	0	0	0	0	0
D16.11LS	0	0	0	0	0	0
D23.11HN	0	0	0	0	0	0
D23.11LN	0	0	0	0	0	0
D15.12HS	0	0	0	0	0	0
D15.12LS	0	0	0	0	0	0
D23.12HN	0	0	0	0	0	0
D23.12LN	0	0	0	0	0	0

Table B3 b: Dunmore

STATION	LITTCAPS	LITTVELI	CIRRNAUP	CIRRCYPR	TERELARV	POLYCILI
D11.12HS	0	0	52	0	0	0
D18.12HN	4	0	0	0	0	0
D18.12LN	8	0	4	0	0	0
D12.01HS	0	0	0	0	0	0
D12.01LS	18	0	0	0	0	0
D19.01HN	0	0	0	0	0	0
D19.01LN	0	0	0	0	0	0
D27.01HS	0	0	0	0	0	0
D27.01LS	0	0	0	0	0	0
D03.02HN	0	0	0	0	0	0
D03.02LN	0	0	0	0	0	0
D11.03HS	50	4	4	38	0	0
D11.03LS	7	0	0	0	0	0
D17.03HN	2	0	7	0	0	0
D17.03LN	0	0	4	0	0	0
D26.03HS	0	75	22	0	0	0
D26.03LS	2	0	0	0	0	0
D02.04HN	0	4	237	0	0	0
D02.04LN	0	0	0	0	0	0
D10.05HS	2	2	14	125	9	611
D10.05LS	2	2	0	2	0	0
D17.05HN	0	0	8	55	4	14
D17.05LN	2	0	0	2	0	6
D24.05HS	0	0	199	295	60	700
D24.05LS	0	0	0	0	0	26
D31.05HN	4	0	12	20	0	125
D31.05LN	0	0	0	0	0	0
D08.07HS	22	0	8	0	0	4
D26.08HS	0	0	4	0	0	0
D06.09HS	0	0	23	2	0	5
D06.09LS	0	0	18	0	0	0
D13.09HN	0	0	2	0	0	0
D13.09LN	0	0	2	0	0	0
D20.09HS	0	0	19	31	0	30
D20.09LS	0	0	43	0	0	24
D27.09HN	0	0	0	0	0	0
D27.09LN	0	0	0	0	0	0
D03.11HS	0	0	3	0	0	0
D03.11LS	0	0	0	0	0	0
D09.11HN	0	0	2	0	0	0
D09.11LN	0	0	0	0	0	0
D16.11HS	0	0	2	0	0	0
D16.11LS	0	0	2	0	0	0
D23.11HN	0	0	0	0	0	0
D23.11LN	0	0	4	0	0	0
D15.12HS	0	0	4	0	0	0
D15.12LS	0	0	0	0	0	0
D23.12HN	0	0	2	0	0	0
D23.12LN	0	0	0	0	0	0

Table B3 c: Dunmore

STATION	PSEUELON	TEMOLONG	CENTHAMA	CALAHELG	SAGIELEG	DIKODIOI
D11.12HS	144	33	0	0	0	0
D18.12HN	48	0	0	0	0	0
D18.12LN	0	0	0	0	0	0
D12.01HS	0	26	0	0	0	0
D12.01LS	0	0	0	0	0	0
D19.01HN	0	0	0	0	0	0
D19.01LN	0	0	0	0	0	0
D27.01HS	0	0	0	0	0	0
D27.01LS	0	0	0	0	0	0
D03.02HN	0	0	0	0	0	0
D03.02LN	0	0	0	0	0	0
D11.03HS	0	4	0	0	0	0
D11.03LS	0	0	0	0	0	0
D17.03HN	4	0	0	0	0	0
D17.03LN	170	0	0	0	0	0
D26.03HS	8	6	0	0	0	0
D26.03LS	0	0	0	0	0	0
D02.04HN	2	2	0	0	0	0
D02.04LN	0	0	0	0	0	0
D10.05HS	223	163	317	0	2	0
D10.05LS	0	0	0	0	0	0
D17.05HN	0	0	16	0	0	0
D17.05LN	0	0	0	0	0	0
D24.05HS	226	174	178	4	13	0
D24.05LS	0	0	0	0	0	0
D31.05HN	4	6	10	0	0	0
D31.05LN	0	0	0	0	0	0
D08.07HS	27	4	4	4	0	0
D26.08HS	0	0	0	0	0	0
D06.09HS	2	0	0	0	0	0
D06.09LS	0	0	0	0	0	0
D13.09HN	2	0	2	0	0	0
D13.09LN	0	0	0	0	0	0
D20.09HS	0	7	2	0	2	10
D20.09LS	0	0	0	0	0	5
D27.09HN	0	0	0	0	0	0
D27.09LN	0	0	0	0	0	0
D03.11HS	81	6	0	0	0	0
D03.11LS	0	0	0	0	0	0
D09.11HN	45	9	0	0	0	0
D09.11LN	0	0	0	0	0	0
D16.11HS	34	2	0	0	2	0
D16.11LS	0	0	0	0	0	0
D23.11HN	0	0	0	0	0	0
D23.11LN	0	0	0	0	0	0
D15.12HS	12	0	0	0	0	0
D15.12LS	0	0	0	0	0	0
D23.12HN	2	2	0	0	0	0
D23.12LN	0	2	0	0	0	0

Table B3 d: Dunmore

STATION	ACARINER	ACARTONS	ACARLONG	ACARCLAU	ACARCOPE	OITHSIMI
D11.12HS	6	0	0	0	20	137
D18.12HN	0	0	0	0	0	75
D18.12LN	0	0	0	0	0	0
D12.01HS	0	0	0	0	4	31
D12.01LS	0	0	0	0	0	0
D19.01HN	0	0	0	0	0	0
D19.01LN	0	0	0	0	0	0
D27.01HS	0	0	0	0	0	0
D27.01LS	8	0	0	0	0	0
D03.02HN	0	0	0	0	4	0
D03.02LN	0	0	0	0	0	0
D11.03HS	0	0	4	0	0	0
D11.03LS	0	0	0	0	0	0
D17.03HN	0	0	0	0	0	0
D17.03LN	0	0	0	0	0	0
D26.03HS	0	0	0	0	9	22
D26.03LS	0	0	0	0	0	0
D02.04HN	4	0	0	0	11	4
D02.04LN	0	0	0	0	0	0
D10.05HS	2	0	2	0	0	16
D10.05LS	0	0	0	0	0	0
D17.05HN	30	0	41	0	108	0
D17.05LN	0	0	0	0	0	0
D24.05HS	95	0	665	0	456	186
D24.05LS	0	0	0	0	0	0
D31.05HN	4	0	0	0	2	10
D31.05LN	0	0	0	0	0	0
D08.07HS	4	0	0	0	0	198
D26.08HS	0	19	0	0	24	0
D06.09HS	0	207	0	0	197	7
D06.09LS	0	18	3	0	12	0
D13.09HN	0	16	81	27	99	5
D13.09LN	0	11	0	0	0	0
D20.09HS	0	542	12	0	1962	31
D20.09LS	0	31	0	0	17	0
D27.09HN	0	0	0	0	0	0
D27.09LN	0	0	0	0	0	0
D03.11HS	8	17	3	0	9	47
D03.11LS	0	0	0	0	0	0
D09.11HN	0	0	9	0	0	15
D09.11LN	0	0	0	0	0	2
D16.11HS	0	4	0	0	88	62
D16.11LS	0	0	0	0	0	2
D23.11HN	0	0	2	0	0	0
D23.11LN	0	0	0	0	0	6
D15.12HS	0	0	0	0	8	98
D15.12LS	0	0	0	0	0	0
D23.12HN	2	0	0	0	4	10
D23.12LN	0	0	0	0	0	0

Table B3 e: Dunmore

STATION	NEOMINTE	DIAPGRAC	DAPHSPEC	BOSMSPEC	CHYDSPEC	CYCLSPEC
D11.12HS	0	0	6	0	0	0
D18.12HN	0	0	0	0	0	0
D18.12LN	0	0	0	0	0	0
D12.01HS	0	0	0	0	0	0
D12.01LS	0	0	0	0	0	4
D19.01HN	0	0	0	0	0	0
D19.01LN	0	53	4	4	0	58
D27.01HS	0	0	0	0	0	0
D27.01LS	0	141	17	59	0	0
D03.02HN	0	0	0	0	0	0
D03.02LN	0	22	0	27	0	0
D11.03HS	0	0	0	0	0	0
D11.03LS	0	16	2	7	0	0
D17.03HN	0	0	4	0	0	0
D17.03LN	0	0	0	0	0	0
D26.03HS	0	0	0	0	0	0
D26.03LS	0	2	0	0	0	0
D02.04HN	0	0	0	0	0	0
D02.04LN	0	0	0	0	0	0
D10.05HS	0	0	0	0	0	0
D10.05LS	0	0	0	0	0	0
D17.05HN	0	0	0	0	0	0
D17.05LN	4	0	0	0	0	0
D24.05HS	0	0	0	0	0	0
D24.05LS	4	0	0	0	0	2
D31.05HN	0	0	0	0	0	0
D31.05LN	2	0	0	0	0	0
D08.07HS	4	0	0	0	0	0
D26.08HS	324	0	0	0	0	0
D06.09HS	0	0	0	0	0	0
D06.09LS	0	0	0	6	0	0
D13.09HN	4	0	0	0	0	0
D13.09LN	22	0	0	2	0	0
D20.09HS	12	0	0	0	0	0
D20.09LS	0	0	0	2	0	2
D27.09HN	0	0	0	0	0	0
D27.09LN	2	0	0	0	0	0
D03.11HS	8	0	0	0	0	0
D03.11LS	4	0	0	0	0	0
D09.11HN	0	0	0	0	0	0
D09.11LN	24	0	0	0	0	0
D16.11HS	0	0	0	0	0	0
D16.11LS	30	0	0	0	0	0
D23.11HN	16	0	0	0	0	0
D23.11LN	44	2	0	0	2	4
D15.12HS	0	0	0	0	0	0
D15.12LS	4	0	0	0	0	0
D23.12HN	0	0	0	2	0	0
D23.12LN	0	34	0	0	0	0

Table B3 f: Dunmore

STATION	EAFADUL	EAFSCOPE	EAFJUVE	HARPSPEC	ROTISPEC	COPENAUP
D11.12HS	46	209	980	183	379	438
D18.12HN	26	879	1804	293	10674	0
D18.12LN	0	38	223	204	5269	0
D12.01HS	358	408	1209	496	74867	589
D12.01LS	159	612	5784	1511	48180	111
D19.01HN	20	584	403	28	1145	0
D19.01LN	57	32	168	37	752	0
D27.01HS	4	89	678	26	47019	0
D27.01LS	17	50	1107	75	12912	0
D03.02HN	23	176	200	13	47881	0
D03.02LN	850	165	536	22	49522	0
D11.03HS	77	773	1766	25	130	1484
D11.03LS	194	230	1367	336	96	427
D17.03HN	2	1248	414	8	0	46
D17.03LN	858	2585	2665	73	0	491
D26.03HS	42	194	1015	220	52144	7336
D26.03LS	194	2134	8686	119	309	648
D02.04HN	308	5634	6314	68	204	1393
D02.04LN	495	16538	162762	4981	2921	2022
D10.05HS	522	6292	2066	68	68	354
D10.05LS	12	158	187	2127	0	22
D17.05HN	6	25990	17628	69	63	717
D17.05LN	5184	21560	232	1695	0	0
D24.05HS	1739	7521	1738	18	783	1500
D24.05LS	3152	33673	84564	11382	11956	0
D31.05HN	205	2780	3476	500	12	741
D31.05LN	5812	52830	36420	0	2572	0
D08.07HS	77	362	515	143	0	180
D26.08HS	0	0	0	0	0	342
D06.09HS	0	0	0	9	0	1023
D06.09LS	15	6	27	15	0	68
D13.09HN	0	9	30	34	0	1354
D13.09LN	7	27	278	653	0	162
D20.09HS	4	14	0	0	0	1657
D20.09LS	26	48	284	2	50	391
D27.09HN	2	6	13	2	0	9
D27.09LN	5	137	235	17	7	50
D03.11HS	202	783	71	36	45	81
D03.11LS	0	4	50	0	0	0
D09.11HN	178	6405	406	6	182	208
D09.11LN	21	379	3577	66	3062	471
D16.11HS	235	2119	92	115	111	376
D16.11LS	189	910	8985	4938	7157	4254
D23.11HN	240	762	344	82	64	10
D23.11LN	12	46	30	142	1597	56
D15.12HS	154	812	30	20	2245	261
D15.12LS	253	456	1407	88	10490	6
D23.12HN	120	772	578	21	4034	105
D23.12LN	155	84	183	145	32	153

Table B4 a: Kincardine

STATION	ETEOLARV	NERELARV	MARAWIRE	MARAEGGS	MARATROC	BIVALARV
K11.12HS	0	0	0	0	0	0
K18.12HN	0	0	0	0	0	0
K18.12LN	0	0	0	0	0	0
K12.01HS	0	0	0	0	0	4
K12.01LS	0	0	18	0	0	0
K19.01HN	0	0	0	0	0	0
K19.01LN	0	0	0	0	0	0
K27.01HS	0	0	0	0	0	0
K27.01LS	0	0	0	0	0	0
K03.02HN	0	0	32	0	2	0
K03.02LN	0	0	5	0	0	0
K11.03HS	0	0	10604	0	2379	0
K11.03LS	0	0	4414	4063	502	0
K17.03HN	0	0	35806	3	15	0
K17.03LN	0	0	198	0	0	0
K26.03HS	0	0	3535	361	1219	0
K26.03LS	0	0	1929	948	903	0
K02.04HN	0	0	108	4	3	0
K02.04LN	0	0	139	3	1	7
K10.05HS	0	14	0	0	0	0
K10.05LS	0	181	6	0	0	59
K17.05HN	0	0	0	0	0	0
K17.05LN	26	250	0	0	0	68
K24.05HS	0	0	0	0	0	6
K24.05LS	0	14	0	0	0	16
K31.05HN	0	0	0	0	0	2
K31.05LN	20	36	0	0	0	248
K08.07HS	2	0	0	0	0	14
K26.08HS	0	0	0	0	0	0
K06.09HS	26	0	0	0	0	0
K13.09HN	0	0	0	0	0	4
K13.09LN	0	0	0	0	0	3
K20.09LS	0	0	0	0	0	0
K27.09HN	0	0	0	0	0	0
K27.09LN	0	0	0	0	0	0
K03.11HS	0	0	0	0	0	0
K09.11HN	0	0	0	0	0	0
K09.11LN	0	0	0	0	0	0
K16.11HS	0	0	0	0	0	0
K16.11LS	0	0	0	0	0	2
K23.11HN	0	0	0	0	0	0
K23.11LN	0	0	0	0	0	0
K15.12HS	0	0	0	0	0	0
K15.12LS	0	0	0	0	0	0
K23.12HN	0	0	0	0	0	0
K23.12LN	0	0	0	0	0	0

Table B4 b: Kincardine

STATION	LITTCAPS	LITVELI	CIRRNAUP	CIRRCYPR	TERELARV	POLYCILI
K11.12HS	0	0	32	0	0	0
K18.12HN	0	0	26	0	0	0
K18.12LN	0	0	22	0	4	0
K12.01HS	0	0	40	0	0	18
K12.01LS	4	0	27	0	13	0
K19.01HN	0	0	0	0	0	0
K19.01LN	0	0	4	0	0	0
K27.01HS	0	0	9	0	0	0
K27.01LS	0	0	0	0	0	0
K03.02HN	0	0	54	0	0	0
K03.02LN	0	0	5	0	0	0
K11.03HS	0	0	34	2100	0	0
K11.03LS	0	0	0	0	0	0
K17.03HN	0	0	38	0	0	0
K17.03LN	0	0	31	0	0	0
K26.03HS	5	0	113	0	0	0
K26.03LS	6	0	11	0	0	0
K02.04HN	4	0	47	0	0	0
K02.04LN	2	0	16	0	0	0
K10.05HS	10	0	406	4	34	199
K10.05LS	0	0	3	0	0	0
K17.05HN	0	22	104	32	10	4887
K17.05LN	2	0	8	34	4	48
K24.05HS	0	0	695	16	60	615
K24.05LS	0	0	2	0	0	107
K31.05HN	2	38	16	26	20	14480
K31.05LN	0	78	0	147	46	189
K08.07HS	14	4	366	16	0	61
K26.08HS	0	0	127	0	0	0
K06.09HS	0	0	1502	141	0	1556
K13.09HN	0	0	630	29	0	20
K13.09LN	0	0	0	7	0	3
K20.09LS	0	0	2	2	0	0
K27.09HN	0	0	57	0	0	12
K27.09LN	0	0	26	0	0	0
K03.11HS	0	0	31	0	0	9
K09.11HN	0	0	17	0	0	11
K09.11LN	0	0	6	0	0	0
K16.11HS	0	0	6	0	0	8
K16.11LS	0	0	0	0	0	0
K23.11HN	0	8	8	0	0	2
K23.11LN	0	0	0	0	0	0
K15.12HS	0	0	2	0	0	0
K15.12LS	0	0	7	0	7	0
K23.12HN	0	0	15	0	0	2
K23.12LN	0	0	11	2	0	0

Table B4 c: Kincardine

STATION	PSEUELON	TEMOLONG	CENTHAMA	CALAHELG	SAGIELEG	OIKODIOI
K11.12HS	0	0	0	0	0	0
K18.12HN	0	13	0	0	0	0
K18.12LN	0	48	0	0	0	0
K12.01HS	4	53	0	0	0	0
K12.01LS	0	53	0	0	0	0
K19.01HN	0	0	0	0	0	0
K19.01LN	0	16	0	0	0	0
K27.01HS	0	0	0	0	0	0
K27.01LS	0	0	0	0	0	0
K03.02HN	0	18	0	0	0	0
K03.02LN	14	136	0	0	0	0
K11.03HS	4	54	0	0	0	0
K11.03LS	0	0	0	0	0	0
K17.03HN	0	47	0	0	2	0
K17.03LN	0	4	0	0	0	0
K26.03HS	5	2	0	0	0	0
K26.03LS	0	0	0	0	0	0
K02.04HN	0	0	0	0	0	0
K02.04LN	0	0	0	0	0	0
K10.05HS	0	2	2	0	0	0
K10.05LS	0	0	0	0	0	0
K17.05HN	0	6	2	0	0	0
K17.05LN	0	0	0	0	0	0
K24.05HS	4	12	4	0	2	0
K24.05LS	0	0	40	0	0	0
K31.05HN	14	10	6	0	0	0
K31.05LN	0	32	32	0	0	0
K08.07HS	6	22	65	0	0	0
K26.08HS	0	0	0	0	0	0
K06.09HS	6	2	0	0	2	277
K13.09HN	0	0	0	0	0	0
K13.09LN	0	0	0	0	0	0
K20.09LS	0	0	0	0	0	0
K27.09HN	0	0	0	0	0	0
K27.09LN	0	0	0	0	0	0
K03.11HS	172	65	579	0	0	17
K09.11HN	25	2	0	0	0	0
K09.11LN	4	0	0	0	0	0
K16.11HS	2	2	0	0	0	2
K16.11LS	0	0	0	0	0	0
K23.11HN	218	10	0	2	0	0
K23.11LN	2	0	0	0	0	0
K15.12HS	2	2	0	0	0	0
K15.12LS	0	0	0	0	0	0
K23.12HN	42	2	0	0	0	0
K23.12LN	0	0	0	2	0	0

Table B4 d: Kincardine

STATION	ACARINER	ACARTONS	ACARLONG	ACARCLAU	ACARCOPE	OITHSIMI
K11.12HS	0	0	0	0	404	39
K18.12HN	0	0	0	0	189	0
K18.12LN	0	0	0	0	0	0
K12.01HS	0	0	0	0	18	18
K12.01LS	8	0	0	0	0	17
K19.01HN	0	0	0	0	0	0
K19.01LN	0	0	0	0	8	4
K27.01HS	4	0	0	0	0	0
K27.01LS	0	0	0	0	0	0
K03.02HN	31	0	0	0	163	0
K03.02LN	0	0	0	0	4	4
K11.03HS	0	0	0	59	226	5
K11.03LS	0	0	0	0	0	0
K17.03HN	0	0	0	15	135	12
K17.03LN	0	0	0	32	17	2
K26.03HS	118	0	0	5	255	4
K26.03LS	0	0	0	0	0	0
K02.04HN	0	0	0	0	0	0
K02.04LN	0	0	0	0	0	0
K10.05HS	0	0	0	0	95	2
K10.05LS	0	0	0	0	0	0
K17.05HN	203	0	0	0	3173	0
K17.05LN	6	0	0	0	24	0
K24.05HS	228	0	0	24	2668	0
K24.05LS	0	0	0	0	0	0
K31.05HN	0	0	18	0	55	0
K31.05LN	0	0	4	0	32	16
K08.07HS	22	0	86	0	178	44
K26.08HS	0	40	0	0	102	29
K06.09HS	0	28	2	0	66	118
K13.09HN	0	0	0	0	36	7
K13.09LN	0	7	10	0	13	3
K20.09LS	0	10	7	0	17	0
K27.09HN	0	0	0	0	2	2
K27.09LN	0	7	0	0	2	0
K03.11HS	93	104	31	3	699	410
K09.11HN	0	0	4	0	264	2
K09.11LN	0	0	4	0	2	11
K16.11HS	0	0	0	2	151	121
K16.11LS	0	0	0	0	2	6
K23.11HN	26	48	22	6	505	256
K23.11LN	0	0	4	0	2	18
K15.12HS	0	0	0	0	6	41
K15.12LS	0	0	0	0	7	7
K23.12HN	0	0	2	0	265	38
K23.12LN	0	0	0	2	0	2

Table B4 e: Kincardine

STATION	NEOMINTE	DIAPGRAC	DAPHSPEC	BOSMSPEC	CHYDSPEC	CYCLSPEC
K11.12HS	0	0	0	0	0	0
K18.12HN	0	0	0	0	0	0
K18.12LN	0	0	0	0	0	0
K12.01HS	0	0	0	0	0	0
K12.01LS	0	0	0	0	0	0
K19.01HN	0	0	0	0	0	0
K19.01LN	0	0	0	4	0	0
K27.01HS	0	0	0	0	0	0
K27.01LS	0	44	22	1	0	0
K03.02HN	0	0	0	0	0	0
K03.02LN	0	0	0	9	0	0
K11.03HS	0	0	0	0	0	2
K11.03LS	2	8	0	0	0	6
K17.03HN	0	6	0	0	0	0
K17.03LN	0	6	0	0	0	0
K26.03HS	0	0	0	0	0	0
K26.03LS	0	0	0	0	0	0
K02.04HN	0	0	0	0	0	0
K02.04LN	0	0	0	0	0	0
K10.05HS	0	0	0	0	0	0
K10.05LS	0	0	0	0	0	0
K17.05HN	0	0	0	0	0	0
K17.05LN	0	0	0	0	0	0
K24.05HS	0	0	0	0	0	0
K24.05LS	0	0	0	0	0	0
K31.05HN	0	0	0	0	0	0
K31.05LN	0	0	0	0	0	0
K08.07HS	0	0	0	0	0	0
K26.08HS	0	0	0	0	0	0
K06.09HS	0	0	0	0	0	0
K13.09HN	0	0	0	0	0	0
K13.09LN	94	0	0	0	0	0
K20.09LS	2	0	0	0	0	0
K27.09HN	0	0	0	0	0	0
K27.09LN	2	0	0	0	0	0
K03.11HS	0	3	0	0	0	0
K09.11HN	0	0	0	0	0	0
K09.11LN	11	0	0	0	0	0
K16.11HS	0	0	0	0	0	0
K16.11LS	4	0	0	0	0	0
K23.11HN	0	0	0	0	0	0
K23.11LN	2	10	2	0	0	0
K15.12HS	0	0	0	0	0	0
K15.12LS	0	0	0	0	0	0
K23.12HN	0	0	0	0	0	0
K23.12LN	0	0	0	0	0	0

Table B4 f: Kincardine

STATION	EAFFADUL	EAFFCOPE	EAFFJUVE	HARPSPEC	ROTISPEC	COPENAUP
K11.12HS	0	0	45	45	78	3601
K18.12HN	13	49	189	0	316	1708
K18.12LN	17	176	404	61	19775	263
K12.01HS	13	62	443	261	4376	1439
K12.01LS	119	518	1037	2897	80900	341
K19.01HN	0	12	20	78	543	0
K19.01LN	12	217	263	56	64197	24
K27.01HS	0	13	144	13	535	44
K27.01LS	0	0	133	22	3444	0
K03.02HN	0	32	386	18	30504	1412
K03.02LN	0	32	82	23	177133	41
K11.03HS	9	662	3482	0	2283	12899
K11.03LS	32	86	264	82	107	0
K17.03HN	2	100	401	31	56	2227
K17.03LN	122	366	216	26	109	334
K26.03HS	14	79	1828	0	609	3544
K26.03LS	126	2112	2651	50	0	0
K02.04HN	2	20	339	0	99	679
K02.04LN	44	58	234	200	0	454
K10.05HS	12	126	252	135	0	555
K10.05LS	23	877	363	2161	56	62
K17.05HN	12	34	5256	2	94	12073
K17.05LN	34	167	1642	383	3203	903
K24.05HS	0	347	782	16	0	3652
K24.05LS	847	10032	9043	123	30782	0
K31.05HN	24	61	823	2	0	2181
K31.05LN	57	4223	3209	1106	0	823
K08.07HS	8	34	0	92	0	721
K26.08HS	0	4	0	8	0	516
K06.09HS	0	0	0	56	0	1502
K13.09HN	0	2	0	21	0	567
K13.09LN	7	7	17	44	0	544
K20.09LS	24	146	230	14	216	3501
K27.09HN	5	0	5	0	0	83
K27.09LN	2	9	19	5	0	298
K03.11HS	121	1183	37	62	0	0
K09.11HN	0	77	20	0	8	4775
K09.11LN	73	187	9	9	51	77
K16.11HS	8	18	0	34	0	1988
K16.11LS	8	84	547	201	829	141
K23.11HN	100	82	0	14	4	6826
K23.11LN	60	178	42	10	46	20
K15.12HS	349	35	35	2	47	200
K15.12LS	7	37	125	676	1853	235
K23.12HN	63	206	19	6	27	3824
K23.12LN	756	876	38	200	137	111

Table B5 a: Skinflats

STATION	ETEOLARV	NERELARV	MARAWIRE	MARAEGGS	MARATROC	BIVALARV
G11.12HS	0	0	0	0	0	0
G12.01HS	0	0	0	0	0	0
G19.01HN	0	0	0	0	0	20
G27.01HS	0	0	0	0	0	0
G03.02HN	0	0	0	0	0	0
G11.03HS	0	0	9860	1233	319	0
G17.03HN	0	0	3483	0	0	0
G26.03HS	0	0	159277	0	0	0
G02.04HN	0	0	730	0	0	7
G10.05HS	0	15	0	0	0	29
G24.05HS	0	4	0	0	0	0
G31.05HN	8	621	0	0	0	82
G06.09HS	0	0	0	0	0	0
G13.09HN	0	0	0	0	0	0
G20.09HS	0	0	0	0	0	0
G03.11HS	0	0	0	0	0	0
G09.11HN	0	0	0	0	0	0
G16.11HS	0	0	0	0	0	0
G23.11HN	0	0	0	0	0	0
G15.12HS	0	0	0	0	0	0

Table B5 b: Skinflats

STATION	LITTCAPS	LITTVELI	CIRRNAUP	CIRRCYPR	TERELARV	POLYCILI
G11.12HS	0	0	78	0	0	0
G12.01HS	0	0	18	0	0	9
G19.01HN	0	0	0	0	0	12
G27.01HS	0	0	17	0	0	22
G03.02HN	4	0	0	0	0	19
G11.03HS	107	91	104	0	0	0
G17.03HN	9	4	9	0	0	0
G26.03HS	4	61	274	0	0	0
G02.04HN	4	8	9	0	0	3771
G10.05HS	0	0	65	15	2	68
G24.05HS	6	340	138	54	2	4837
G31.05HN	0	0	0	0	4	49
G06.09HS	0	0	16	9	0	26
G13.09HN	0	0	23	20	0	6
G20.09HS	12	0	50	14	0	149
G03.11HS	0	0	11	0	0	0
G09.11HN	0	0	2	0	0	0
G16.11HS	2	0	4	0	0	0
G23.11HN	0	0	0	0	0	0
G15.12HS	0	0	3	2	0	0

Table B5 c: Skinflats

STATION	PSEUELON	TEMOLONG	CENTHAMA	CALAHELG	SAGIELEG	OIKODIOI
G11.12HS	99	6	0	0	0	0
G12.01HS	31	111	0	0	4	0
G19.01HN	0	0	0	0	0	0
G27.01HS	0	65	13	0	4	0
G03.02HN	0	0	0	0	0	0
G11.03HS	210	473	0	7	160	0
G17.03HN	2	20	0	0	2	0
G26.03HS	88	65	0	0	7	0
G02.04HN	4	0	0	0	0	0
G10.05HS	0	0	13	0	0	0
G24.05HS	83	140	143	0	0	0
G31.05HN	0	29	78	0	0	0
G06.09HS	2	5	0	0	2	0
G13.09HN	2	0	0	0	0	0
G20.09HS	28	21	0	0	2	67
G03.11HS	121	65	0	0	6	6
G09.11HN	1559	310	0	0	11	10
G16.11HS	1692	38	0	8	8	8
G23.11HN	74	8	0	2	2	0
G15.12HS	241	4	0	0	8	0

Table B5 d: Skinflats

STATION	ACARINER	ACARTONS	ACARLONG	ACARCLAU	ACARCOPE	OITHSIMI
G11.12HS	20	0	0	0	229	144
G12.01HS	8	0	0	0	27	53
G19.01HN	0	0	0	0	0	0
G27.01HS	96	0	0	0	87	200
G03.02HN	0	0	0	0	4	0
G11.03HS	0	0	0	321	16	89
G17.03HN	201	0	0	31	454	0
G26.03HS	102	0	0	0	113	264
G02.04HN	11	0	0	0	34	4
G10.05HS	6	0	0	0	6	4
G24.05HS	1152	0	0	0	2391	44
G31.05HN	16	0	0	0	0	0
G06.09HS	0	12	0	0	54	49
G13.09HN	0	41	185	36	243	18
G20.09HS	0	460	0	0	302	175
G03.11HS	11	34	0	0	59	748
G09.11HN	24	51	242	13	157	214
G16.11HS	6	0	0	0	68	76
G23.11HN	4	4	0	4	14	0
G15.12HS	6	0	2	37	58	76

Table B5 e: Skinflats

STATION	NEOMINTE	DIAPGRAC	DAPHSPEC	BOSMSPEC	CHYDSPEC	CYCLSPEC
G11.12HS	0	0	0	0	0	0
G12.01HS	0	0	0	0	0	0
G19.01HN	0	0	0	0	0	0
G27.01HS	0	120	0	4	0	0
G03.02HN	0	0	0	0	0	0
G11.03HS	0	0	0	0	0	0
G17.03HN	0	0	0	0	0	0
G26.03HS	0	0	0	0	0	0
G02.04HN	0	0	0	0	0	0
G10.05HS	0	0	0	0	0	2
G24.05HS	0	0	0	0	0	0
G31.05HN	0	0	0	0	0	0
G06.09HS	0	0	0	0	0	0
G13.09HN	0	0	0	0	0	0
G20.09HS	0	0	0	0	0	0
G03.11HS	0	0	0	0	0	0
G09.11HN	0	0	0	0	0	0
G16.11HS	0	0	0	0	0	0
G23.11HN	0	0	0	0	0	0
G15.12HS	2	0	0	0	0	0

Table B5 f: Skinflats

STATION	EAFFADUL	EAFFCOPE	EAFFJUVE	HARPSPEC	ROTISPEC	COPENAUP
G11.12HS	27	85	301	445	1864	811
G12.01HS	44	278	2007	1288	227950	1803
G19.01HN	0	4	0	2196	1628	469
G27.01HS	13	69	13294	726	97360	6673
G03.02HN	0	0	3632	240	5675	1589
G11.03HS	187	180	4110	99	0	1712
G17.03HN	4	507	2271	1349	1834	5000
G26.03HS	25	36	4063	8596	0	4750
G02.04HN	11	580	4606	3502	5562	6292
G10.05HS	15	154	194	5517	35	3457
G24.05HS	261	1239	0	1885	1217	2609
G31.05HN	21	12	0	39910	0	0
G06.09HS	0	5	0	0	91	979
G13.09HN	2	0	0	68	0	1831
G20.09HS	2	10	0	355	0	715
G03.11HS	14	913	6741	163	6067	4045
G09.11HN	0	56	338	67	3340	336
G16.11HS	1312	2483	227	92	10	185
G23.11HN	46	94	46	174	0	246
G15.12HS	80	59	0	33	0	53

Table B6 a: Culcross

STATION	ETEOLARV	NERELARV	MARAWIRE	MARAEGGS	MARATROC	BIVALARV
C11.03HS	0	0	876	1884	399	0
C17.03HN	0	0	55	0	0	0
C26.03HS	0	0	120	10	1	0
C02.04HN	0	0	85	0	0	0
C10.05HS	0	4	0	0	0	0
C17.05HN	0	8	0	0	0	0
C24.05HS	0	0	0	0	0	0
C31.05HN	0	0	0	0	0	0
C08.07HS	0	0	0	0	0	2
C26.08HS	0	0	0	0	0	0
C06.09HS	0	0	0	0	0	0
C13.09HN	0	0	0	0	0	0
C20.09HS	0	0	0	0	0	0
C27.09HN	0	0	0	0	0	0
C03.11HS	0	0	0	0	0	0
C09.11HN	0	0	0	0	0	0
C16.11HS	0	0	0	0	0	0
C23.11HN	0	0	0	0	0	0
C15.12HS	0	0	0	0	0	0
C23.12HN	0	0	0	0	0	0

Table B6 b: Culross

STATION	LITTCAPS	LITTVELI	CIRRNAUP	CIRRCYPR	TERELARV	POLYCILI
C11.03HS	1645	0	134	0	2	0
C17.03HN	55	2	28	0	0	0
C26.03HS	2530	20	63	0	0	0
C02.04HN	40	0	79	0	0	0
C10.05HS	1083	10	4860	192	126	8232
C17.05HN	23	253	967	31	2	271
C24.05HS	4343	9	196	4	24	204
C31.05HN	2349	0	477	8	14	10
C08.07HS	279	5	2290	5	0	59
C26.08HS	0	0	1652	4	0	0
C06.09HS	7	0	976	28	0	0
C13.09HN	0	0	399	0	0	23
C20.09HS	82	0	2244	29	0	34
C27.09HN	0	0	7	0	0	7
C03.11HS	8	0	45	0	0	6
C09.11HN	0	0	13	0	0	0
C16.11HS	0	0	4	0	0	0
C23.11HN	0	0	12	0	0	4
C15.12HS	692	0	222	0	0	6
C23.12HN	0	0	0	0	0	2

Table B6 c: Culross

STATION	PSEUELON	TEMOLONG	CENTHAMA	CALAHELG	SAGIELEG	OIKODIOI
C11.03HS	0	23	2	2	2	0
C17.03HN	0	2	0	2	0	0
C26.03HS	7	6	0	0	0	0
C02.04HN	0	0	0	0	0	0
C10.05HS	29	44	35	8	0	0
C17.05HN	0	0	0	0	0	0
C24.05HS	0	4	0	0	0	0
C31.05HN	0	2	2	0	0	0
C08.07HS	0	0	7	0	0	0
C26.08HS	0	0	0	0	0	0
C06.09HS	2	2	0	0	0	232
C13.09HN	0	2	0	0	0	0
C20.09HS	5	0	0	0	0	10
C27.09HN	0	0	0	0	0	0
C03.11HS	674	56	0	0	6	14
C09.11HN	66	4	0	0	2	0
C16.11HS	103	6	0	0	0	0
C23.11HN	10	2	0	0	0	0
C15.12HS	2	0	0	0	0	0
C23.12HN	2	0	0	0	0	0

Table B6 d: Culross

STATION	ACARINER	ACARTONS	ACARLONG	ACARCLAU	ACARCOPE	OITHSIMI
C11.03HS	82	0	0	0	12	22
C17.03HN	0	0	0	4	20	0
C26.03HS	0	0	0	0	32	32
C02.04HN	0	0	0	0	0	0
C10.05HS	35	0	0	0	286	226
C17.05HN	0	0	0	0	2	0
C24.05HS	20	0	0	0	129	11
C31.05HN	0	0	0	0	2	0
C08.07HS	0	0	5	0	29	5
C26.08HS	0	8	0	0	4	39
C06.09HS	0	2	23	0	63	28
C13.09HN	0	2	5	0	34	2
C20.09HS	0	38	5	0	110	28
C27.09HN	0	0	0	0	2	0
C03.11HS	14	25	39	6	0	432
C09.11HN	60	0	0	11	312	86
C16.11HS	6	2	6	0	16	44
C23.11HN	0	0	0	0	30	12
C15.12HS	0	0	0	0	10	24
C23.12HN	0	0	0	0	2	8

Table B6 e: Culross

STATION	NEOMINTE	DIAPGRAC	DAPHSPEC	BOSMSPEC	CHYDSPEC	CYCLSPEC
C11.03HS	0	0	0	0	0	0
C17.03HN	0	0	0	0	0	0
C26.03HS	0	0	0	0	0	0
C02.04HN	0	0	0	0	0	0
C10.05HS	0	0	0	0	0	0
C17.05HN	0	0	0	0	0	0
C24.05HS	0	0	0	0	0	0
C31.05HN	0	0	0	0	0	0
C08.07HS	0	0	0	0	0	0
C26.08HS	0	0	0	0	0	0
C06.09HS	0	0	0	0	0	0
C13.09HN	0	0	0	0	0	0
C20.09HS	0	0	0	0	0	0
C27.09HN	0	0	0	0	0	0
C03.11HS	0	0	0	0	0	0
C09.11HN	0	0	0	0	0	0
C16.11HS	0	0	0	0	0	0
C23.11HN	0	0	0	0	0	0
C15.12HS	0	0	0	0	0	0
C23.12HN	0	0	0	0	0	0

Table B6 f: Culross

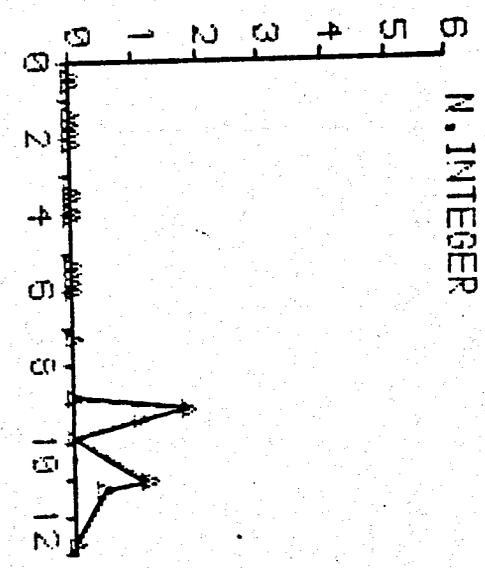
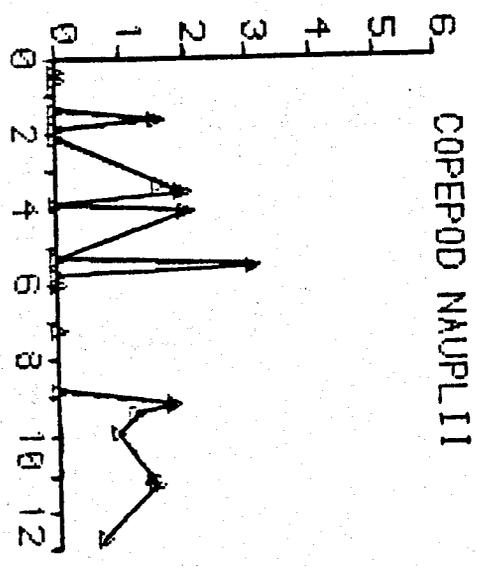
STATION	EAFFADUL	EAFFCOPE	EAFFJUVE	HARPSPEC	ROTISPEC	COPENAUP
C11.03HS	287	100	18	34	103	116
C17.03HN	0	16	240	140	24	1769
C26.03HS	0	9	14	43	0	84
C02.04HN	27	7	112	54	0	263
C10.05HS	0	338	0	159	0	169
C17.05HN	0	10	14	225	0	76
C24.05HS	39	165	126	48	0	302
C31.05HN	0	14	0	119	0	74
C08.07HS	0	5	0	20	0	408
C26.08HS	0	0	0	4	0	176
C06.09HS	2	2	7	178	0	0
C13.09HN	0	9	0	18	0	180
C20.09HS	5	0	0	167	0	895
C27.09HN	0	0	0	2	0	229
C03.11HS	3	205	62	76	404	118
C09.11HN	2	0	9	101	13	113
C16.11HS	606	404	0	46	0	36
C23.11HN	6	0	0	130	776	156
C15.12HS	47	53	18	167	94	404
C23.12HN	0	0	15	48	17	48

Appendix C: Zooplankton abundance: Figures

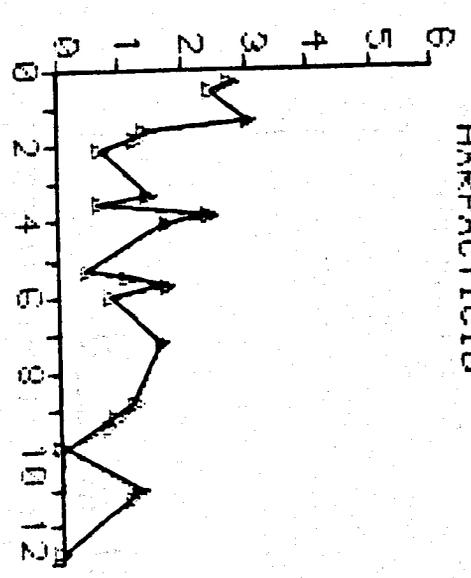


Figure 1: Zooplankton abundance over time. The y-axis represents abundance and the x-axis represents time. The graph shows several peaks and troughs, indicating seasonal or periodic fluctuations in zooplankton numbers.

FALLIN MID_GRP HT



HARPACTICID



ROTIFERA

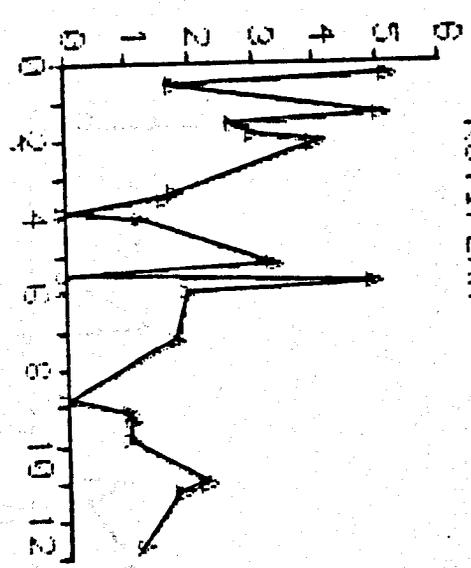
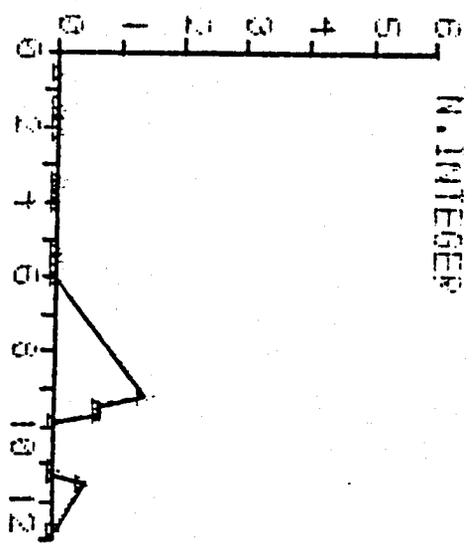
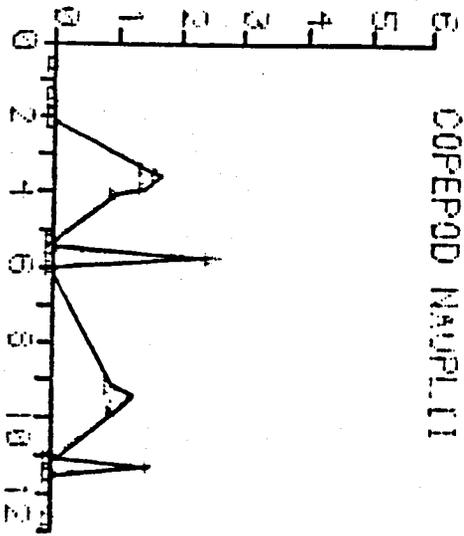
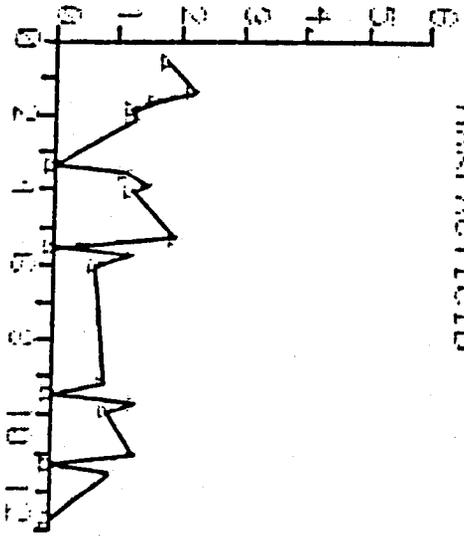


Figure C1 a: Annual abundance of mixed group taxa at Fallin, high tide. Logarithmic scales, Nos/m³

FALLIN MID-SRP LT



Harpacticoid



Rotifera

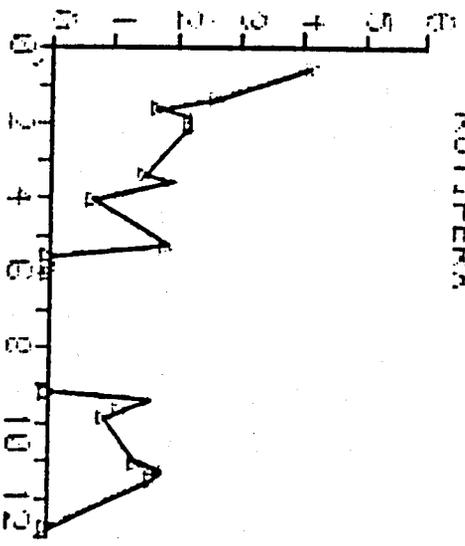


Figure C1 b: Annual abundance of mixed group taxa at Fallin, low tide.
 Logarithmic scales, Nos/m³

S. ALLOA MID_GRP HT

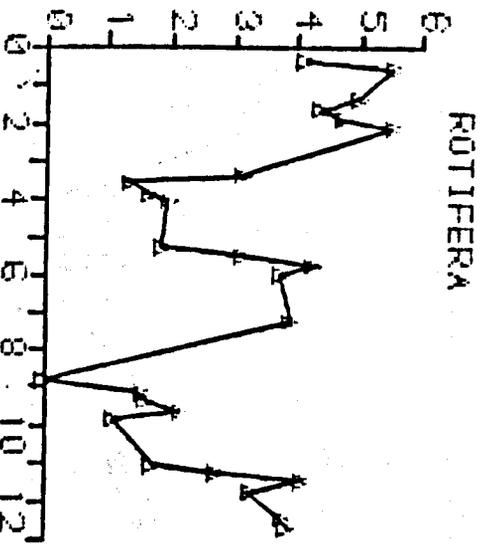
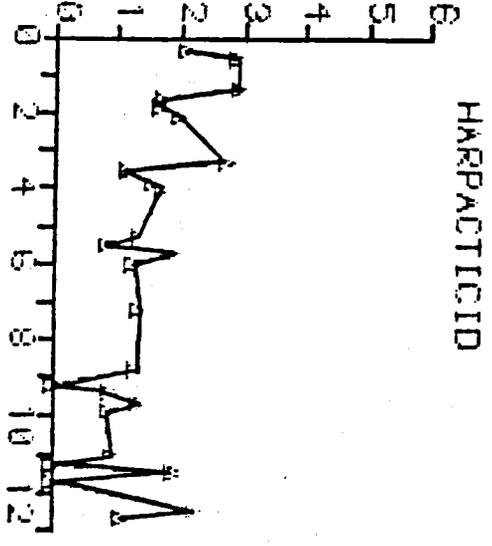
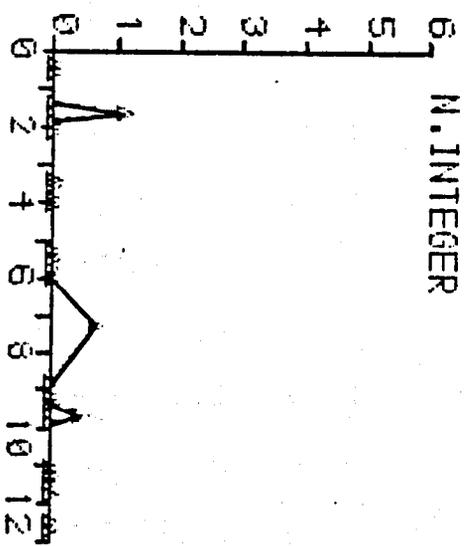
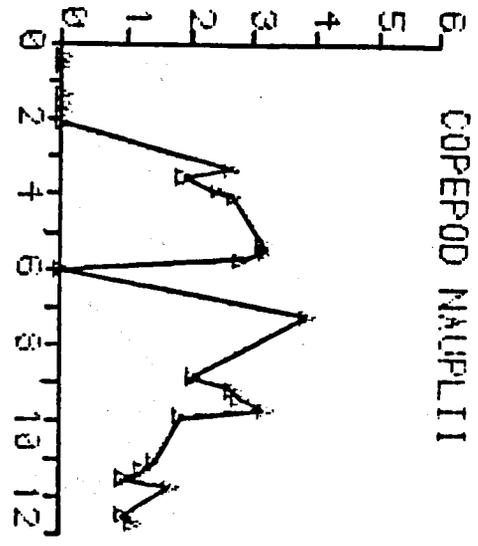
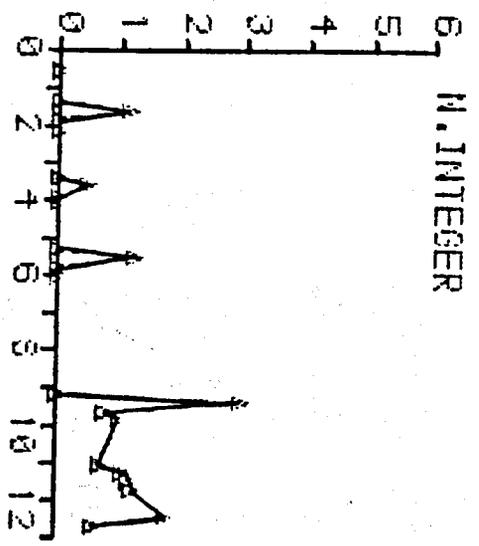
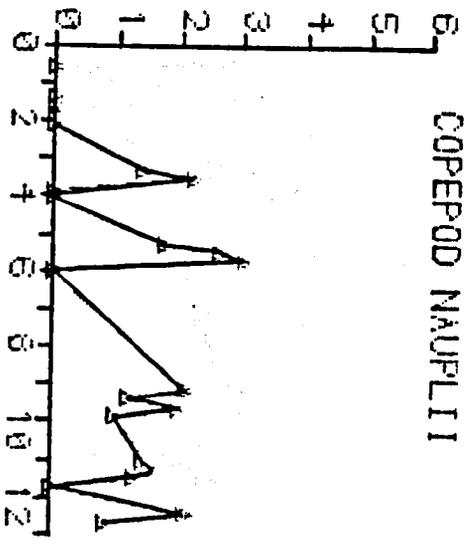
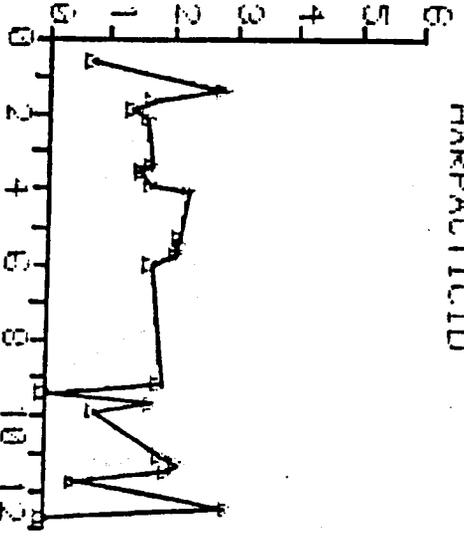


Figure C2 a: Annual abundance of mixed group taxa at South Alloa at high tide. Logarithmic scales, Nos/m³

S. ALLOA MID_GRP LT



HARPACTICID



ROTIFERA

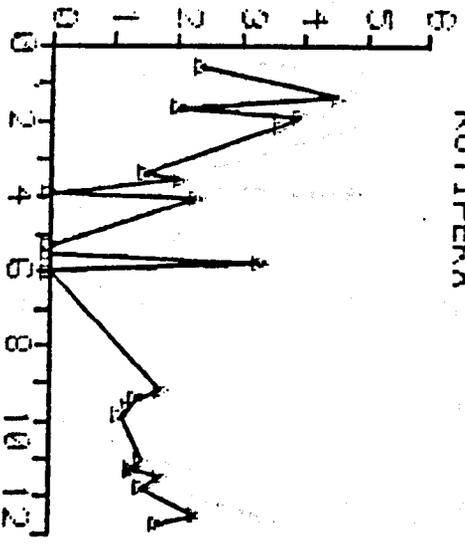
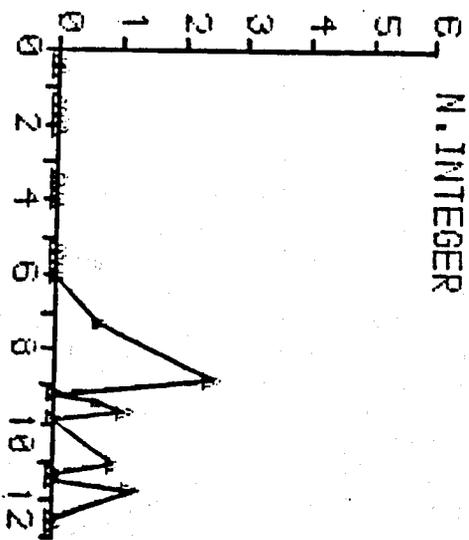
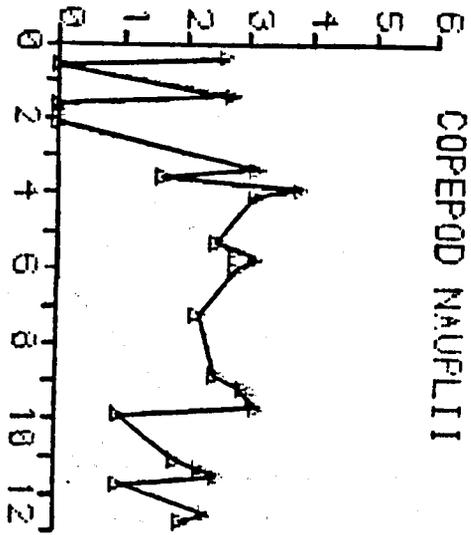
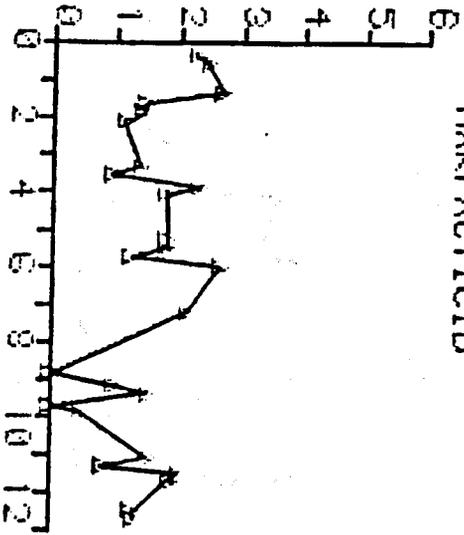


Figure C2 b: Annual abundance of mixed group taxa at South Alloa at low tide. Logarithmic scales, Nos/m³

DUMMORE MID_GRP HT



HARPACTICID



ROTIFERA

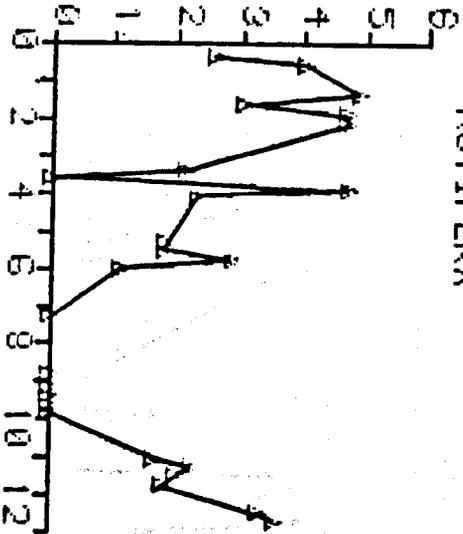


Figure C3 a: Annual abundance of mixed group taxa at Dummore at high tide.
 Logarithmic scale, Nos/m³

DUNMORE MID_GRP LT

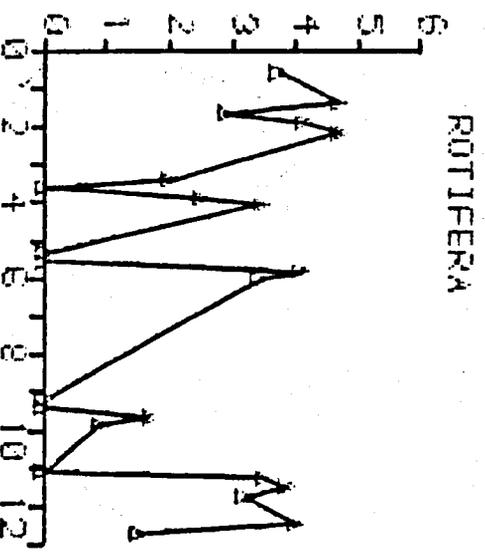
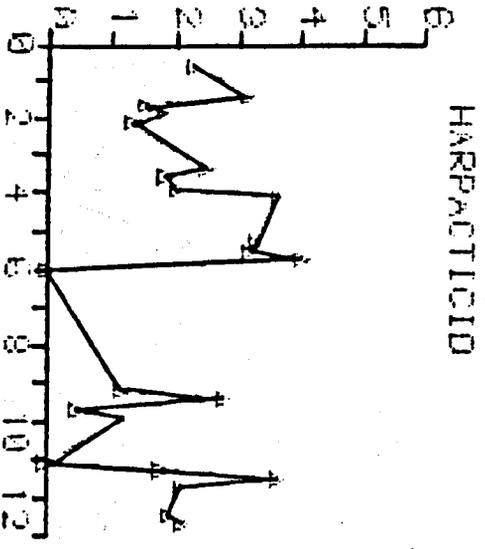
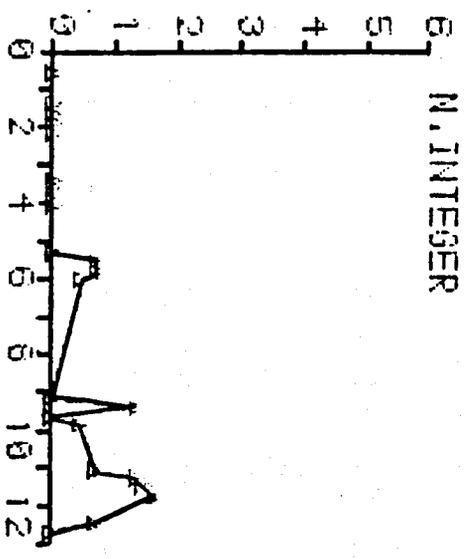
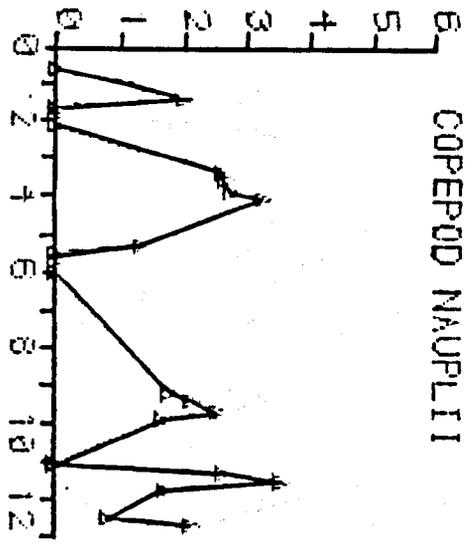


Figure C3 b; Annual abundance of mixed group taxa at Dunmore at low tide. Logarithmic scales, Nos/m³

KINCARDINE MID_GRP HT

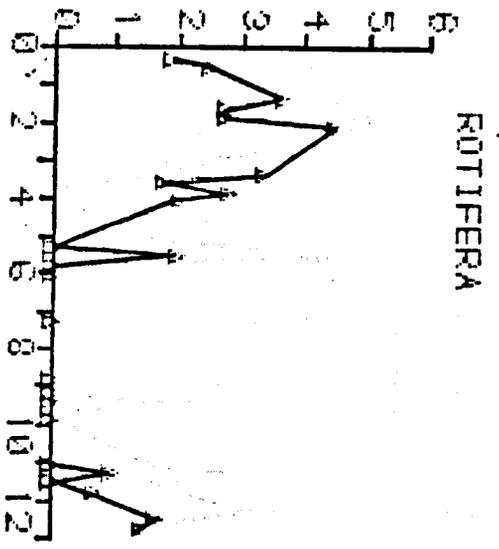
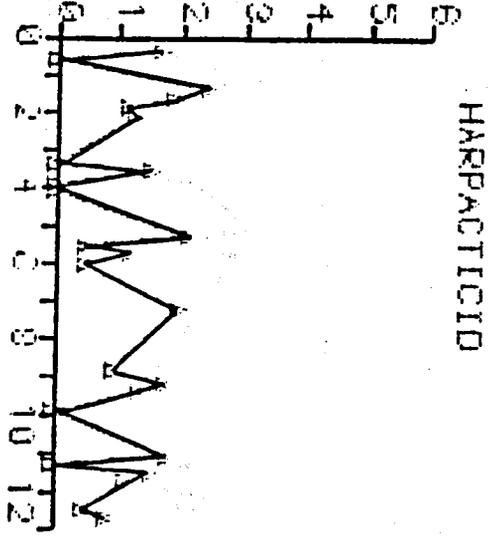
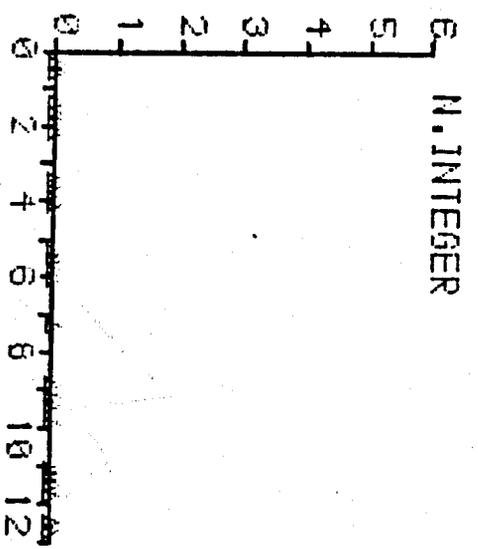
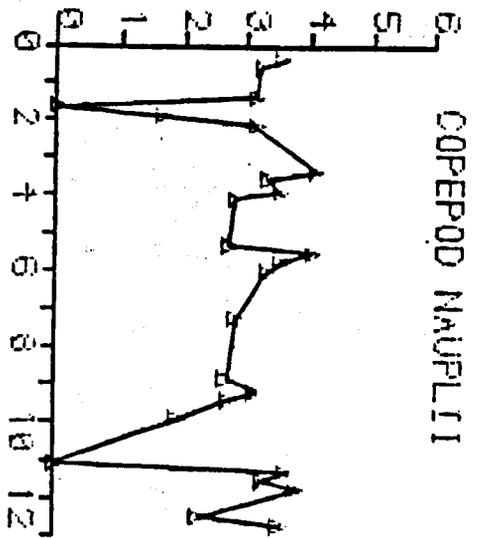
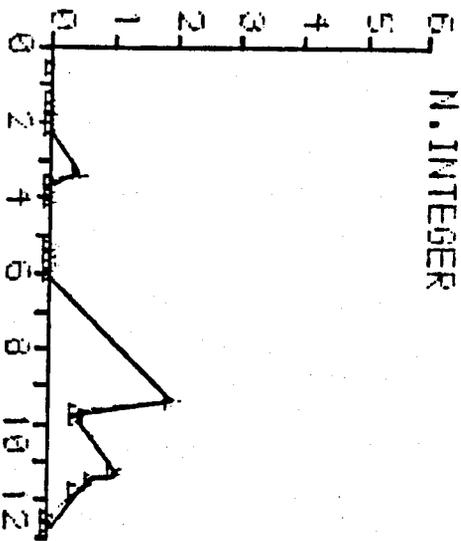
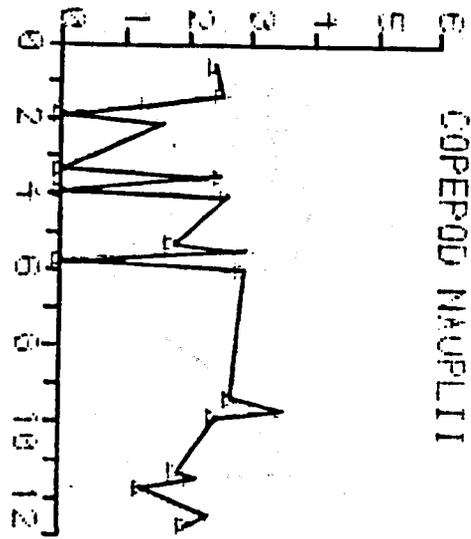
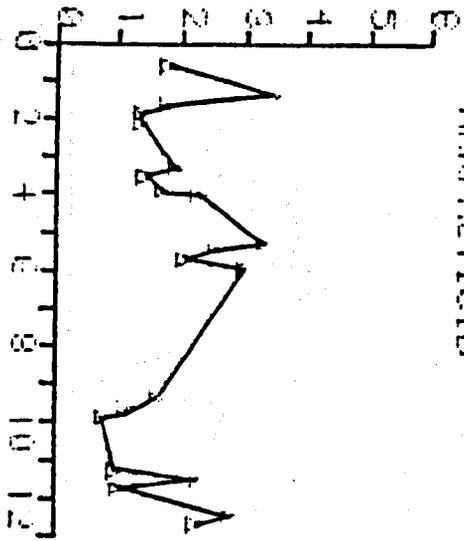


Figure C4 a: Annual abundance of mixed group taxa at Kincardine at high tide. Logarithmic scales, Nos/m³

KINCARDINE MID_GRP LT



HARPACTICID



ROTIFERA

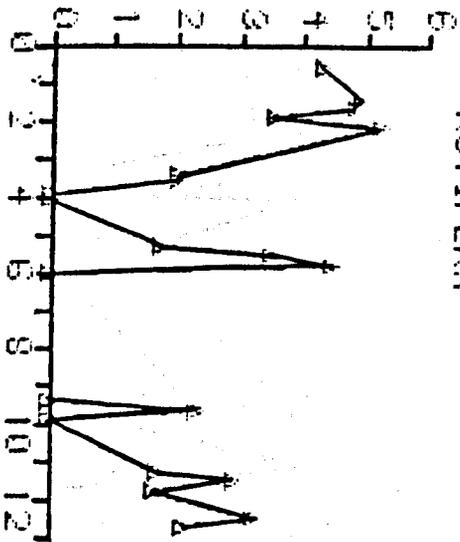


Figure C4 b: Annual abundance of mixed group taxa at Kincardine at low tide. Logarithmic scales, Nos/m³

SKINFLATS MID_GRP HT

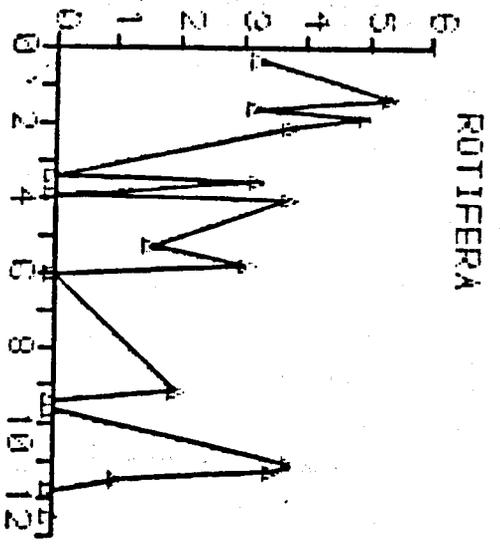
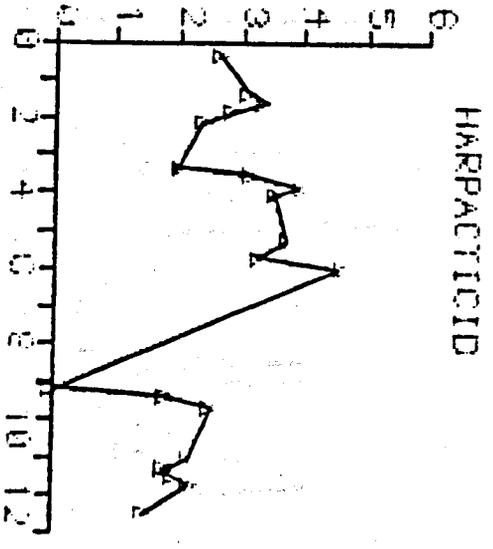
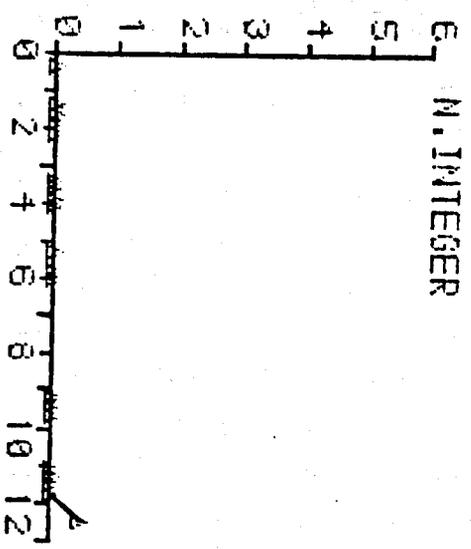
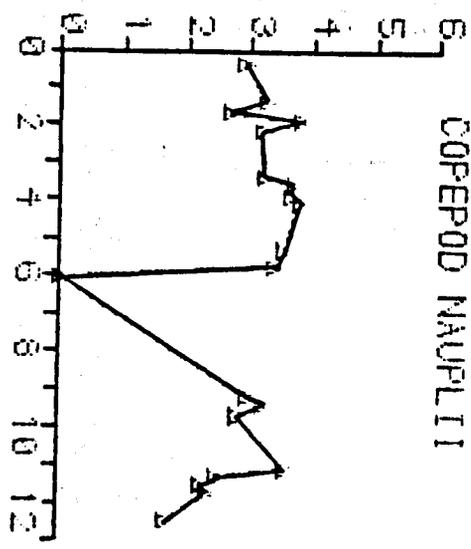


Figure C5 a: Annual abundance of mixed group taxa at Skinflats at high tide. Logarithmic scales, Nos/m³

CULROSS MID_SKP HT

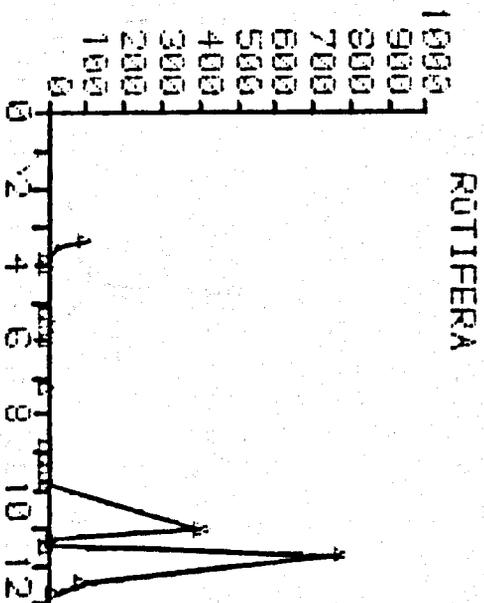
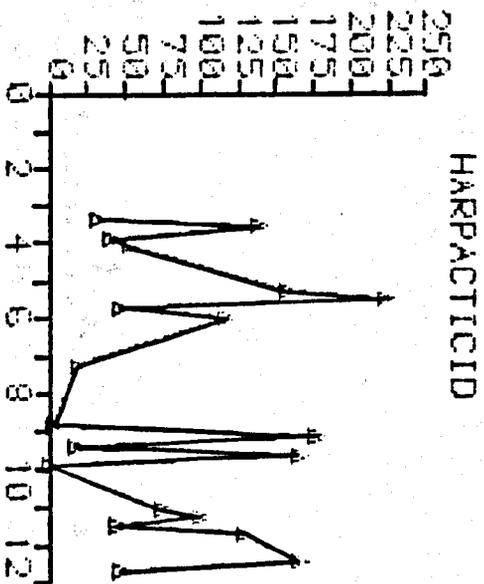
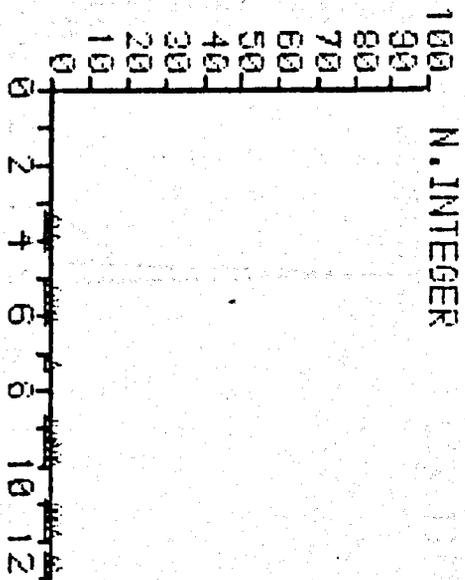
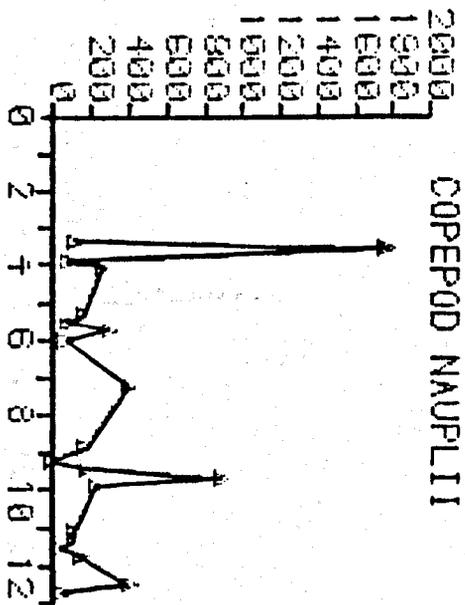


Figure C5 b: Annual abundance of mixed group taxa at Culross at low tide.
 Logarithmic scales, Nos/m³

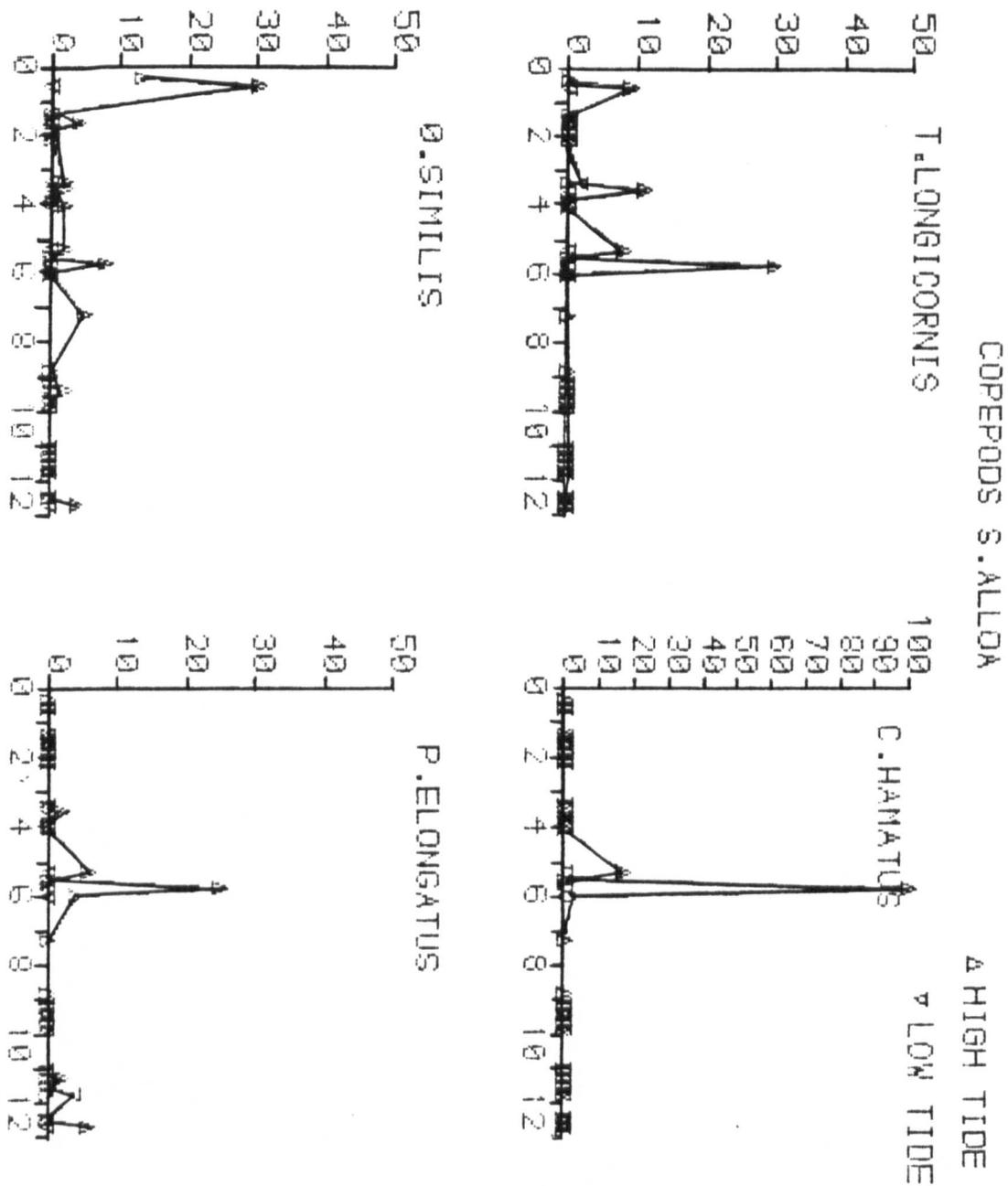


Figure C6: Annual abundance of neritic copepods at South Alloa, high and low tides. Linear scales, Nos/m³

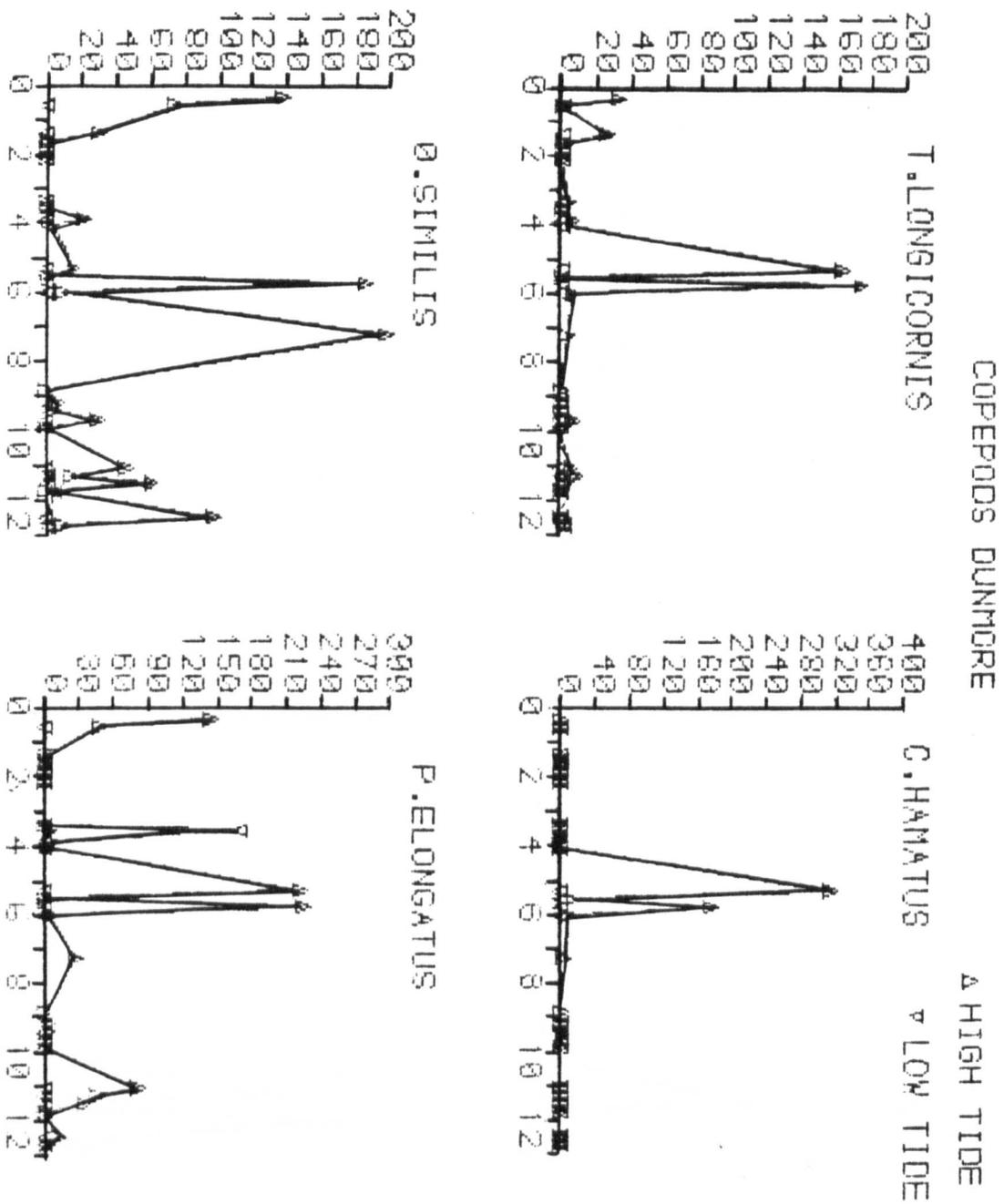


Figure C7: Annual abundance of neritic copepods at Dunmore, high and low tides.
 Linear scales, Nos/m³

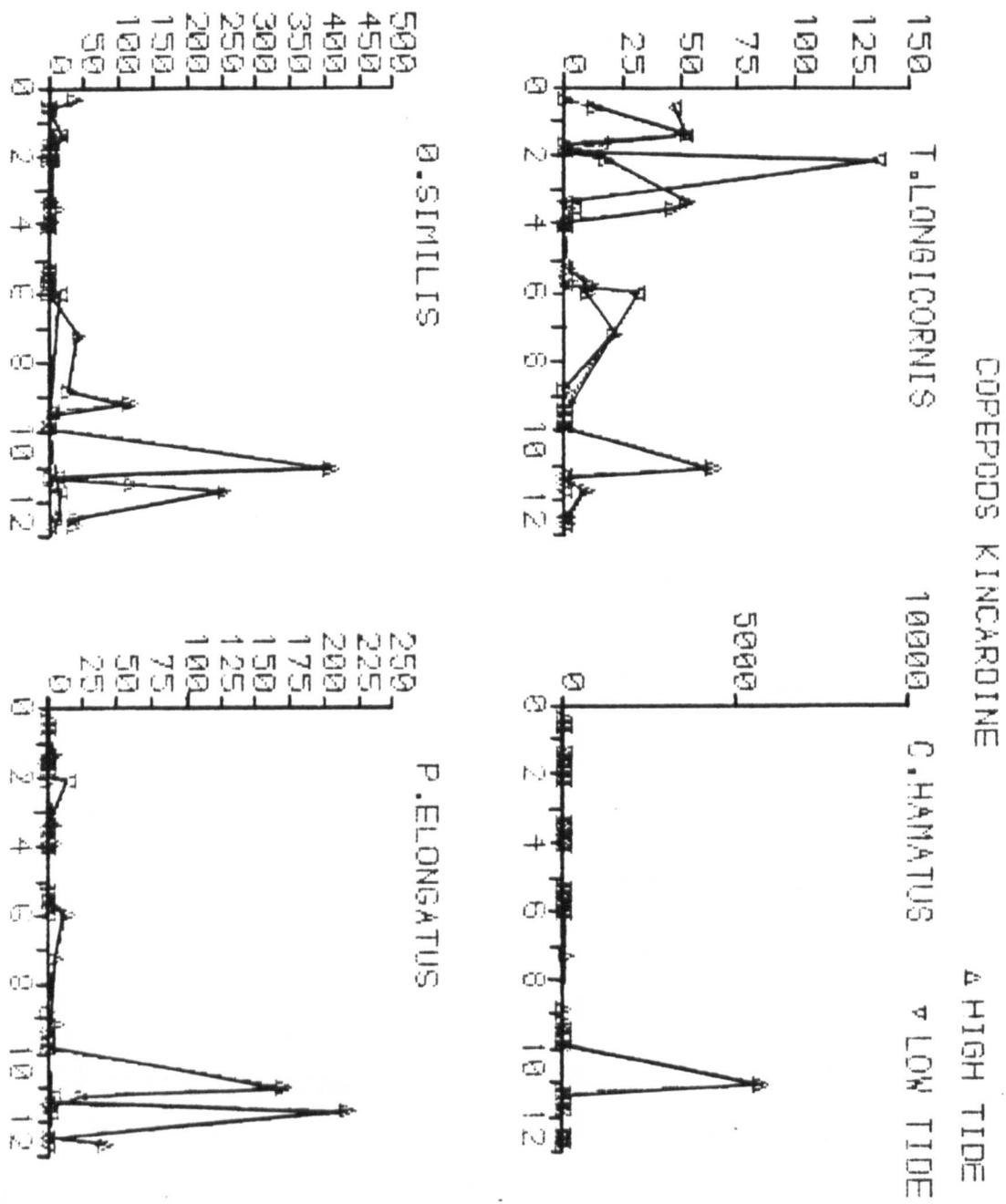


Figure C8: Annual abundance of neritic copepods at Kincardine, high and low tides.
 Linear scales, Nos/m³

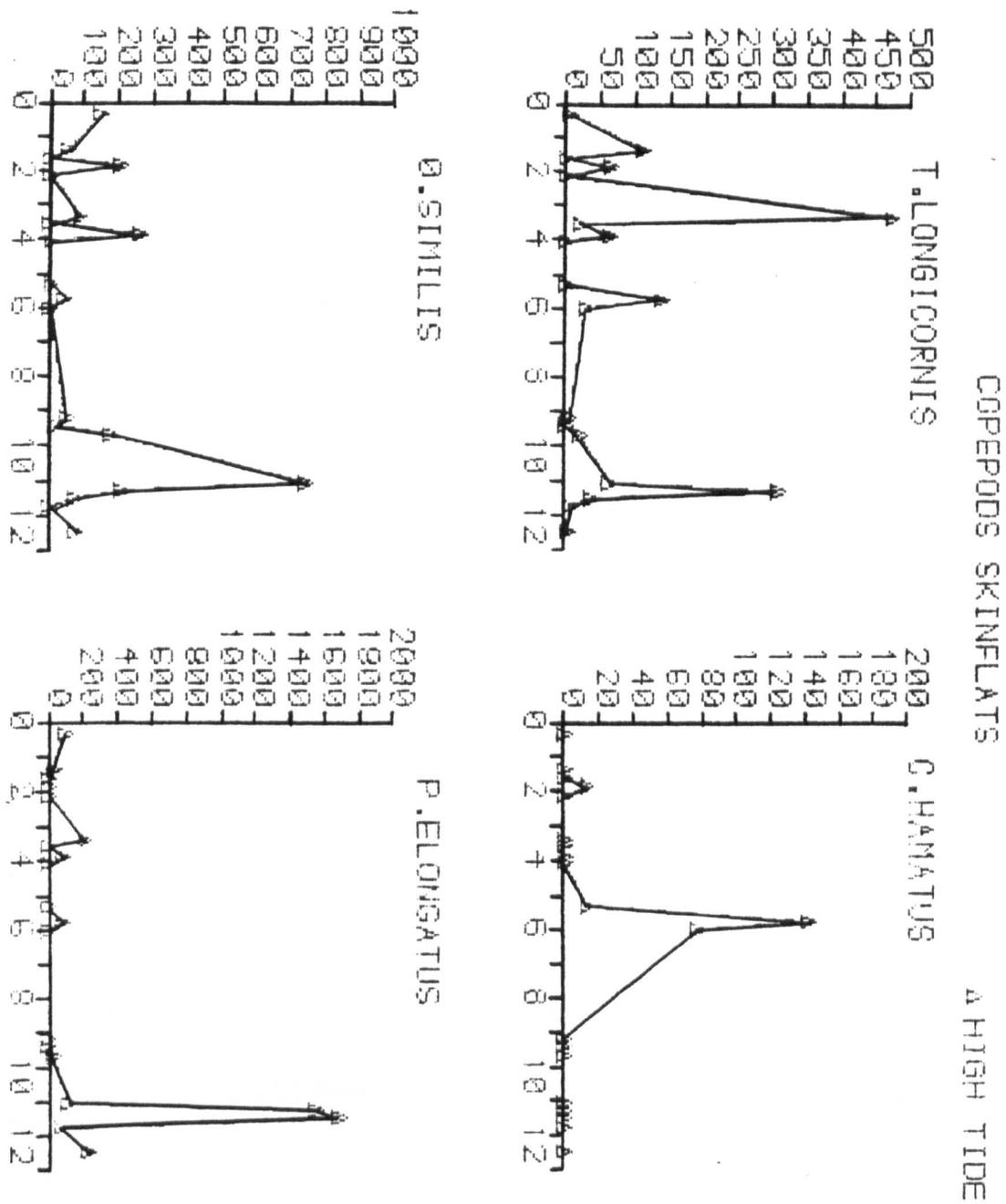


Figure C9: Annual abundance of neritic copepods at Skinflats at high and low tides. Linear scales, Nos/m³

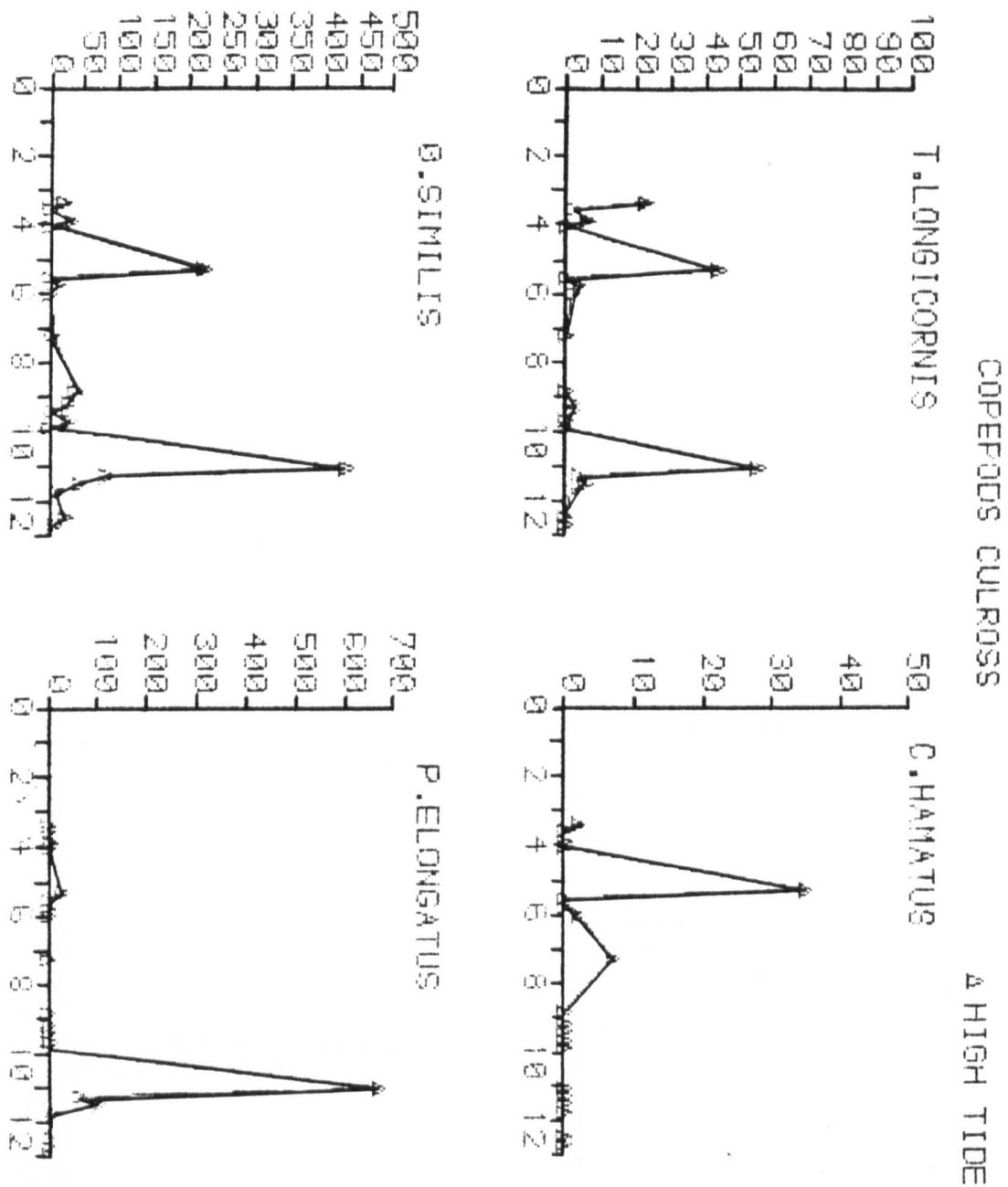


Figure C10: Annual abundance of neritic copepods at Culross at high and low tides. Linear scales, Nos/m³

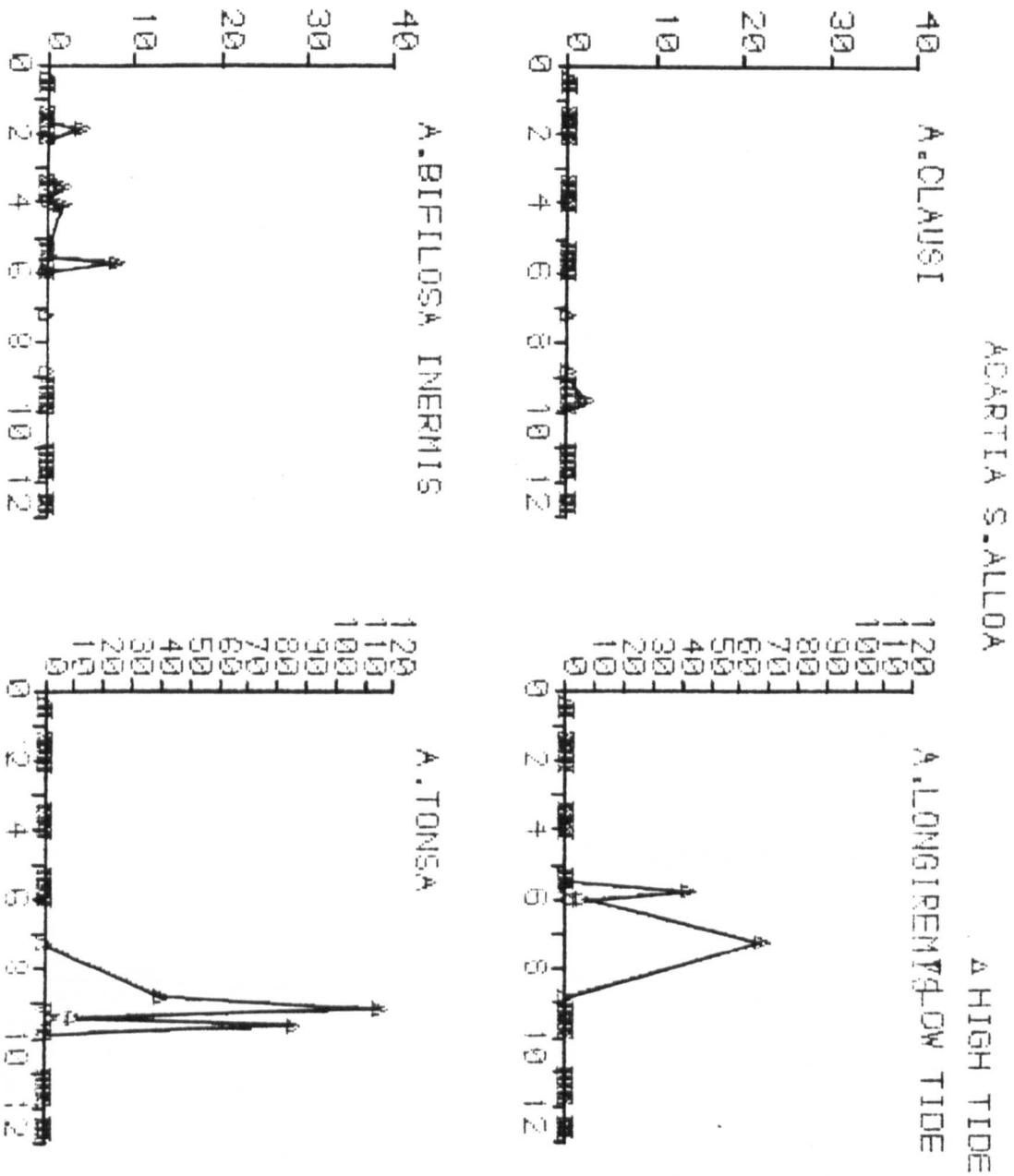


Figure C11: Annual abundance of *Acartia* spp. at South Alloa, high and low tides. Linear scales, Nos/m³

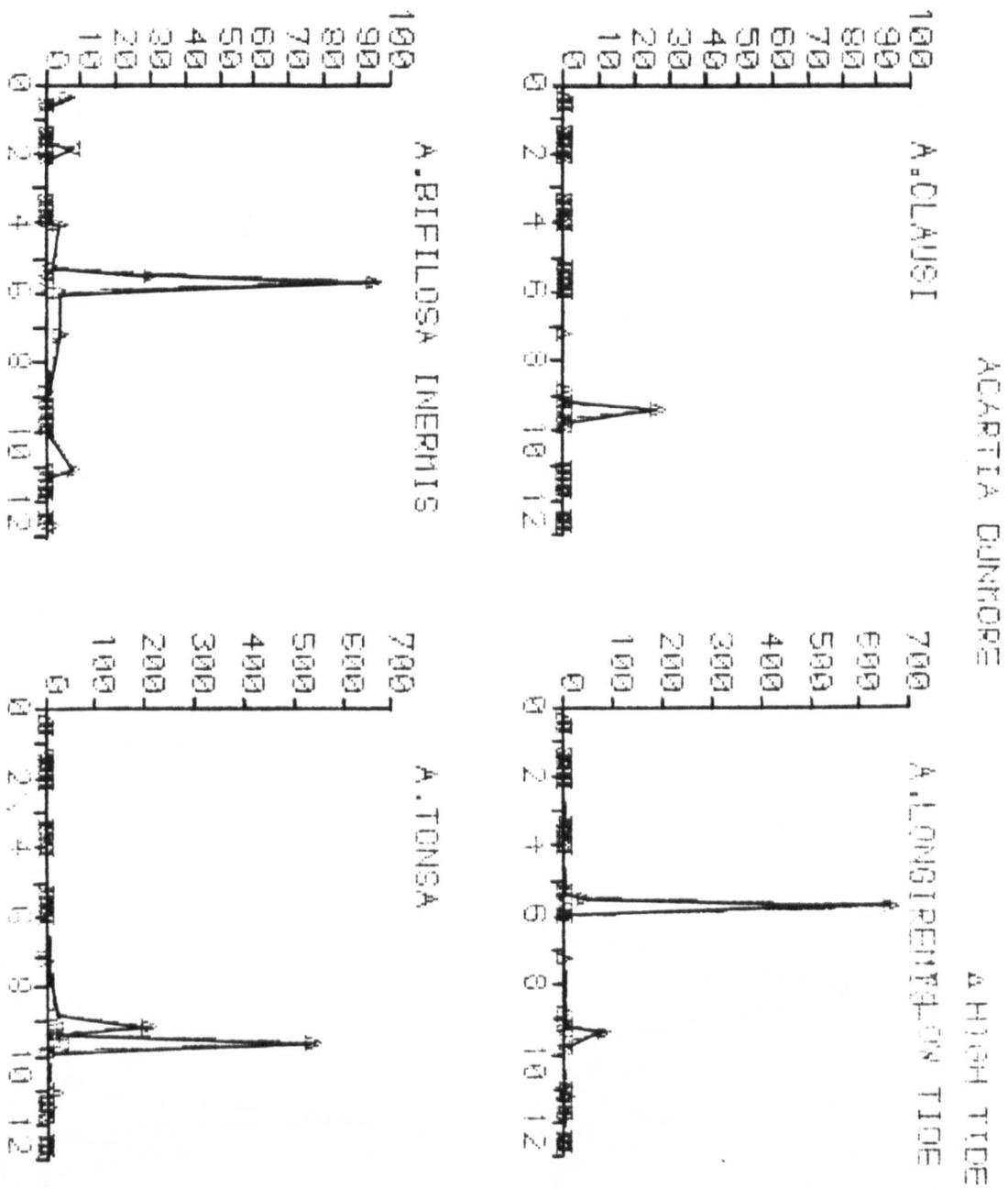
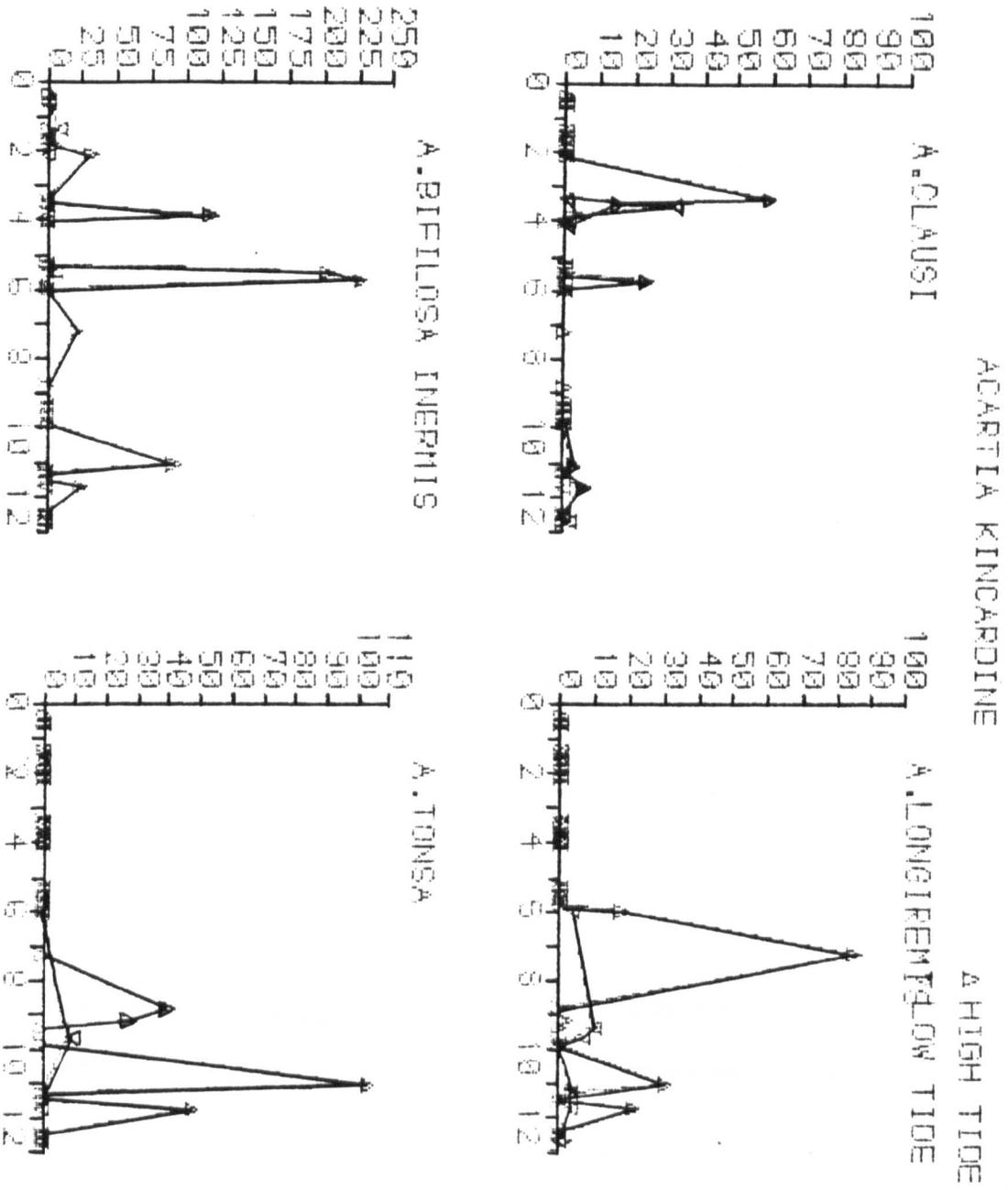


Figure C12: Annual abundance of Acartia spp. at Dunmore, high and low tides. Linear scales, Nos/m³



A. TONSA

Month	Abundance (Nos/m ³)
1	0
2	0
3	0
4	0
5	0
6	0
7	0
8	0
9	0
10	100
11	40
12	0

Figure C13: Annual abundance of *Acartia* spp. at Kincardine, high and low tide. Linear scales, Nos/m³

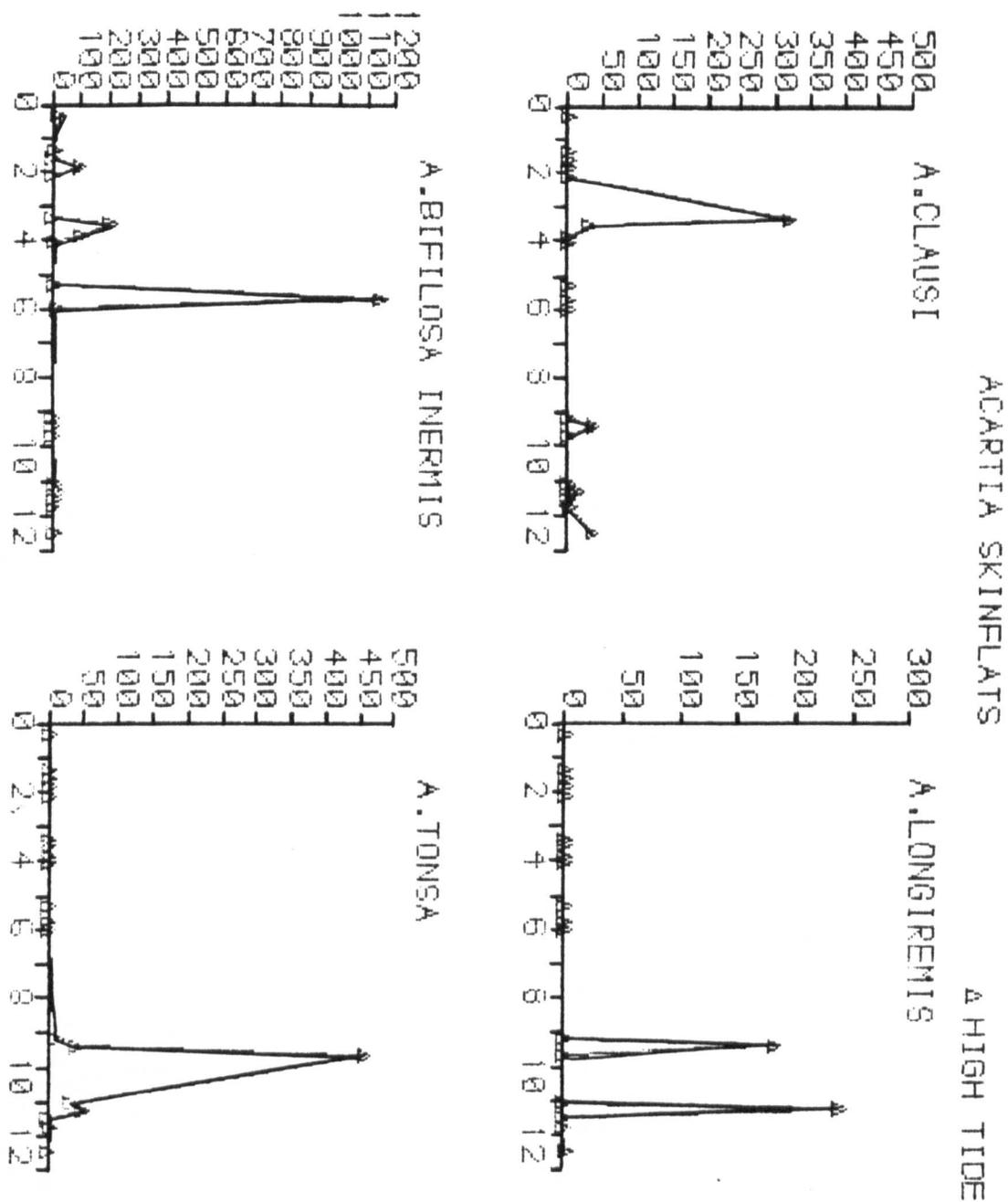


Figure C14: Annual abundance of *Acartia* spp. at Skinflats, high and low tides. Linear scales, Nos/m³

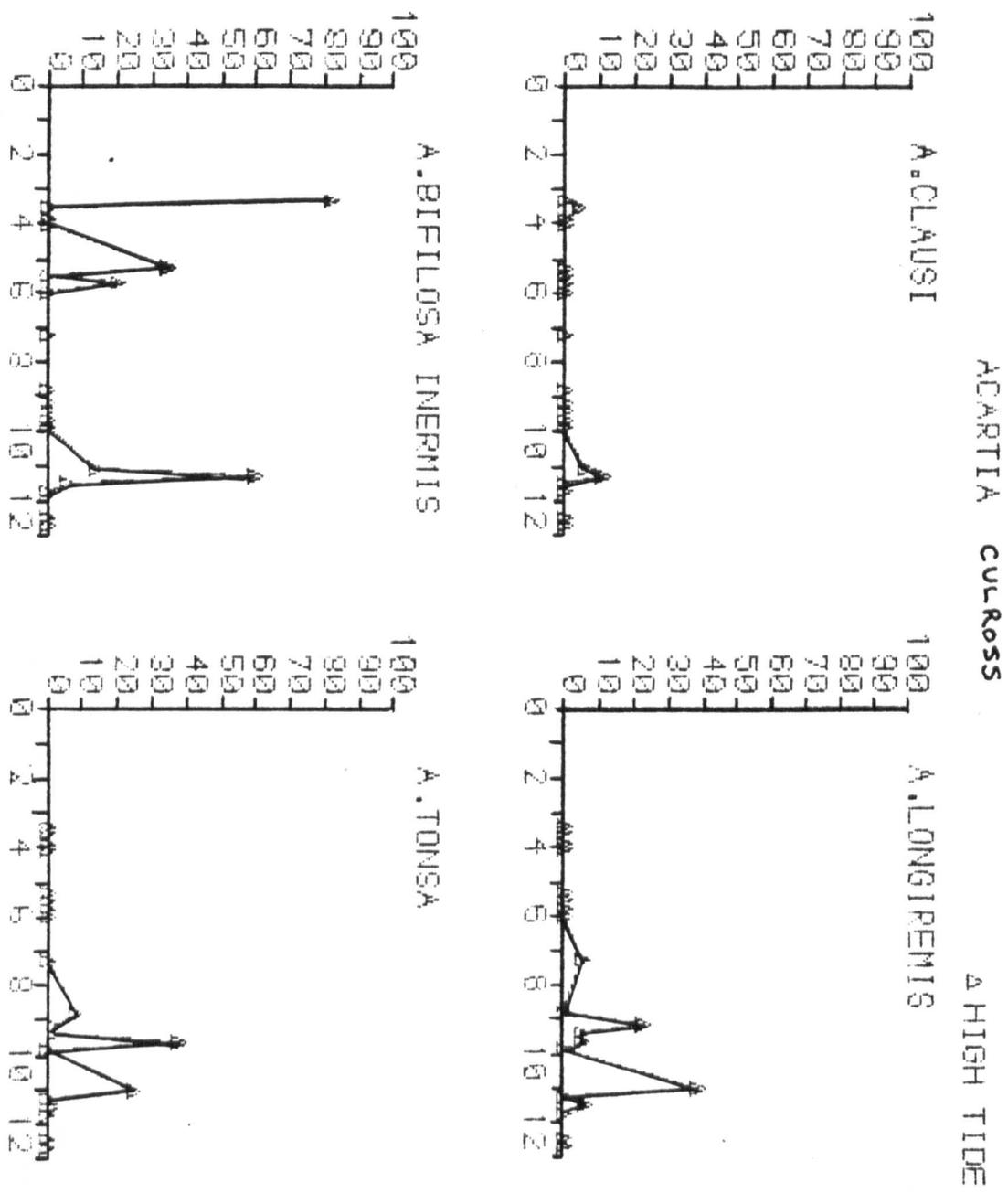


Figure C15: Annual abundance of Acartia spp. at Culross, high and low tides. Linear scales, Nos/m³

FPW FALLIN HIGH TIDE

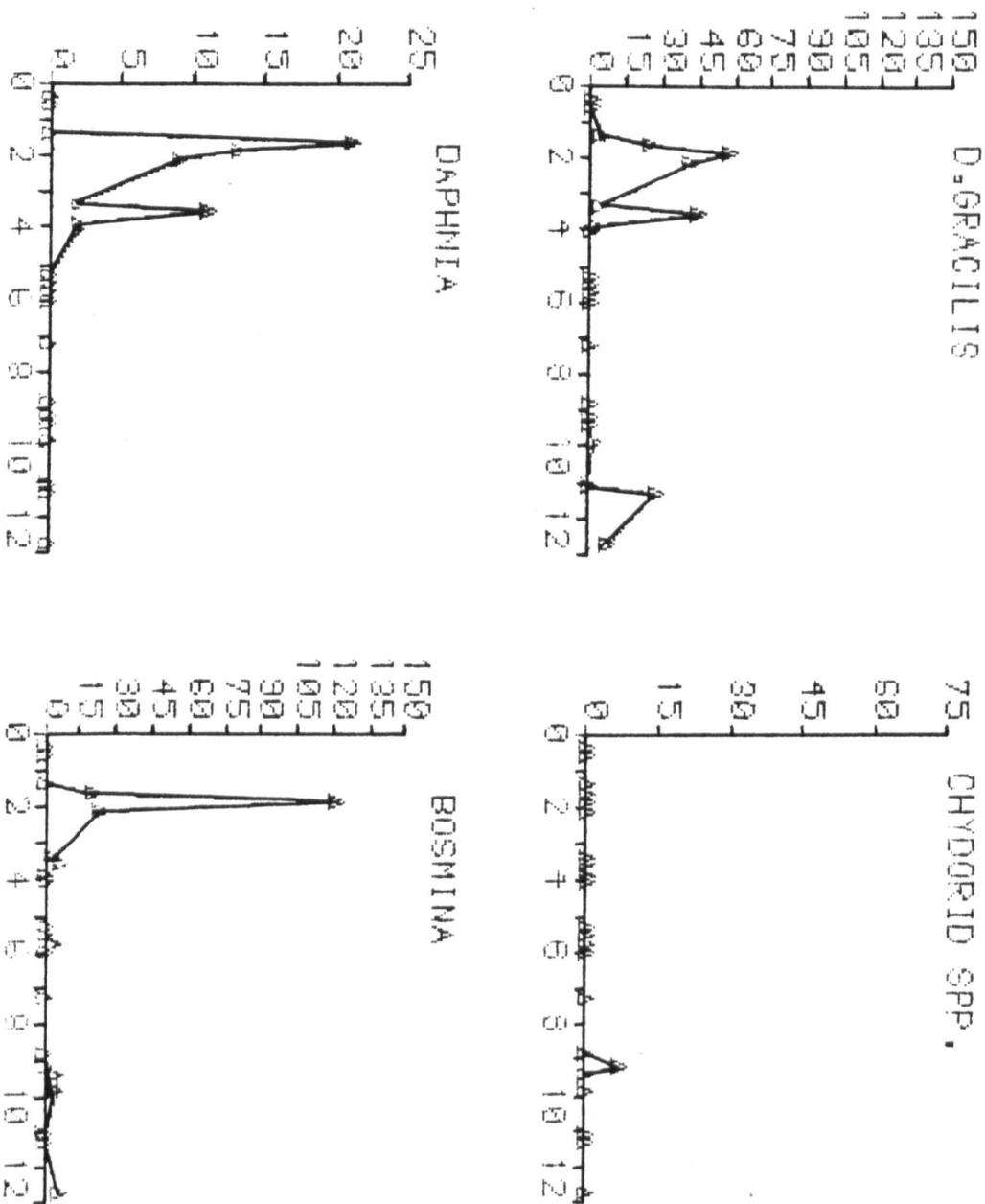


Figure C16 a: Annual abundance of freshwater taxa at Fallin at high tide.
 Linear scales, Nos/m³

FRW FALLIN LOW TIDE

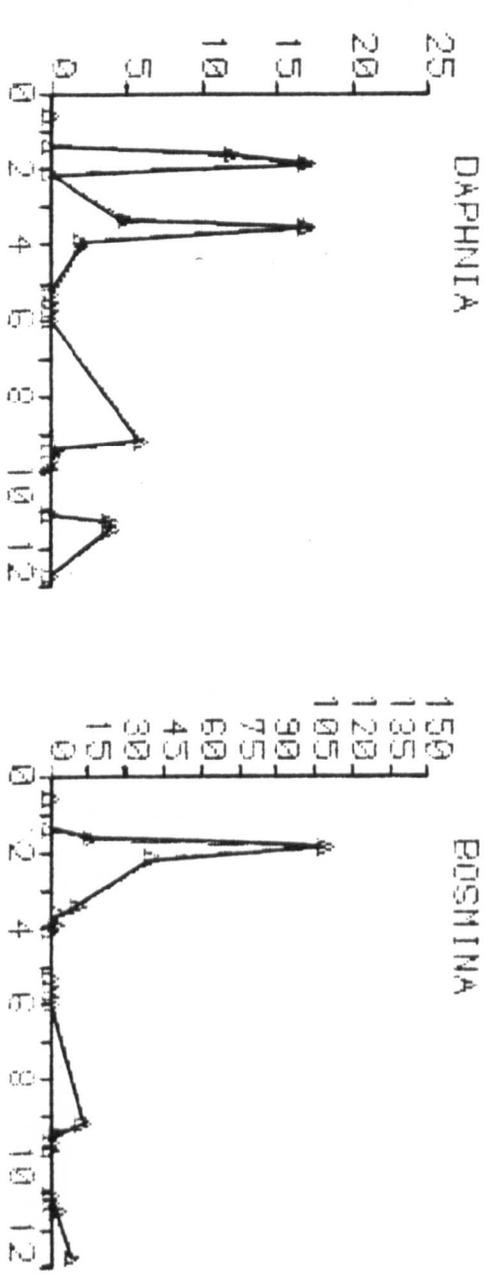
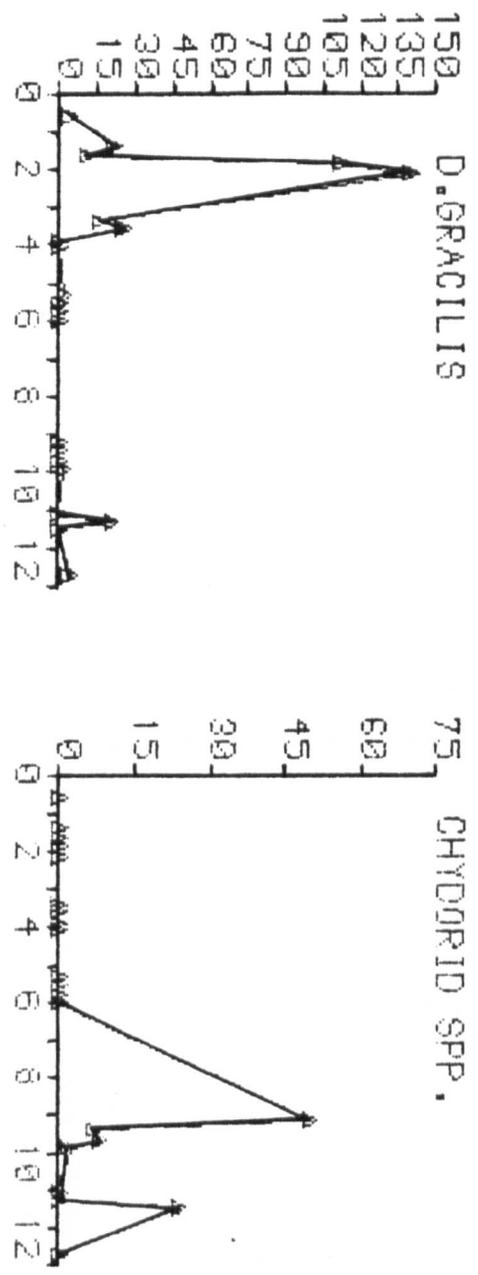


Figure C16 b: Annual abundance of freshwater taxa at Fallin at low tide.
 Linear scales, Nos/m³

FRESHWATER TAXA AT HIGH TIDE

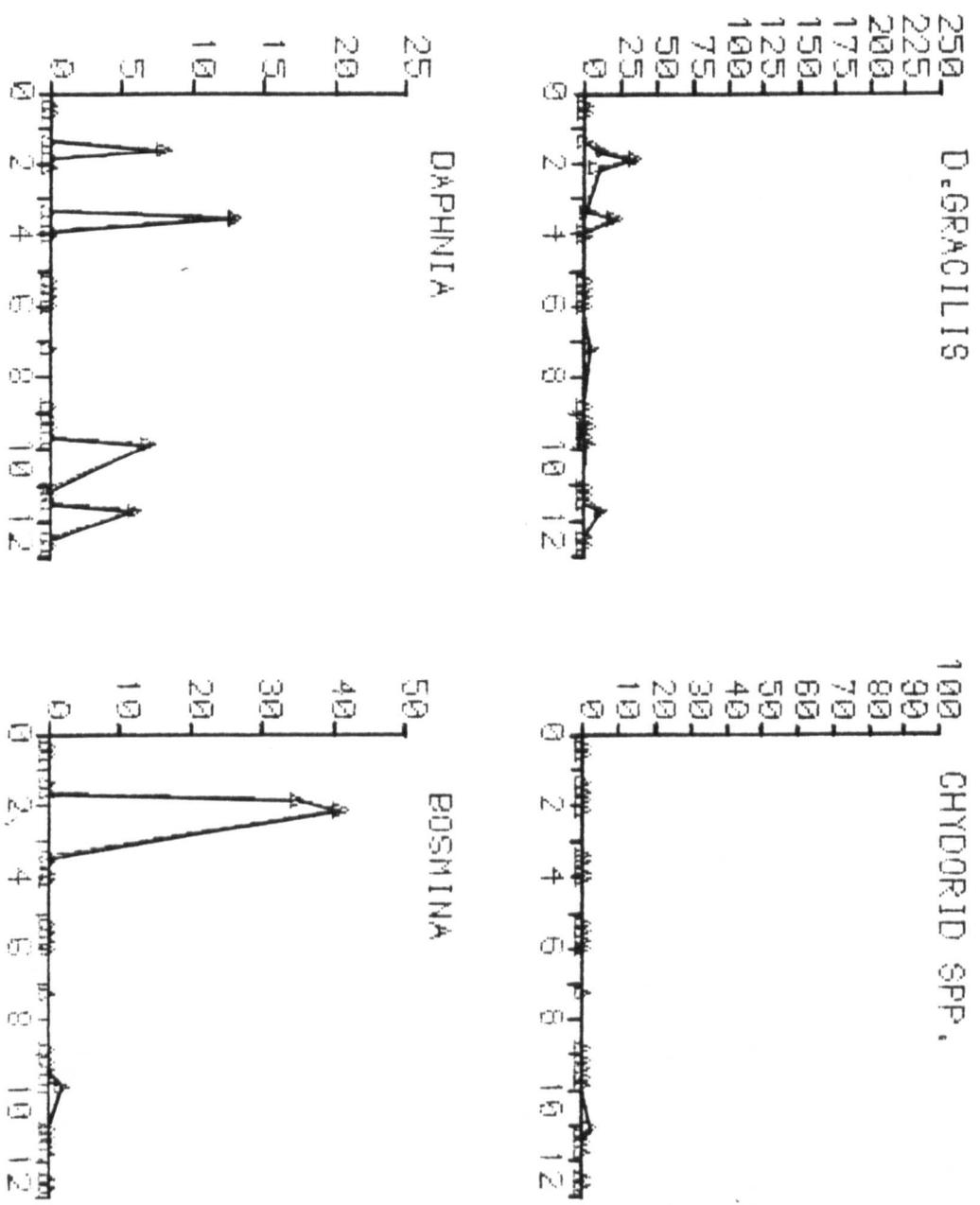


Figure C17 a: Annual abundance of freshwater taxa at South Alloa at high tide. Linear scales, Nos/m³

FRW S. ALLOA LOW TIDE

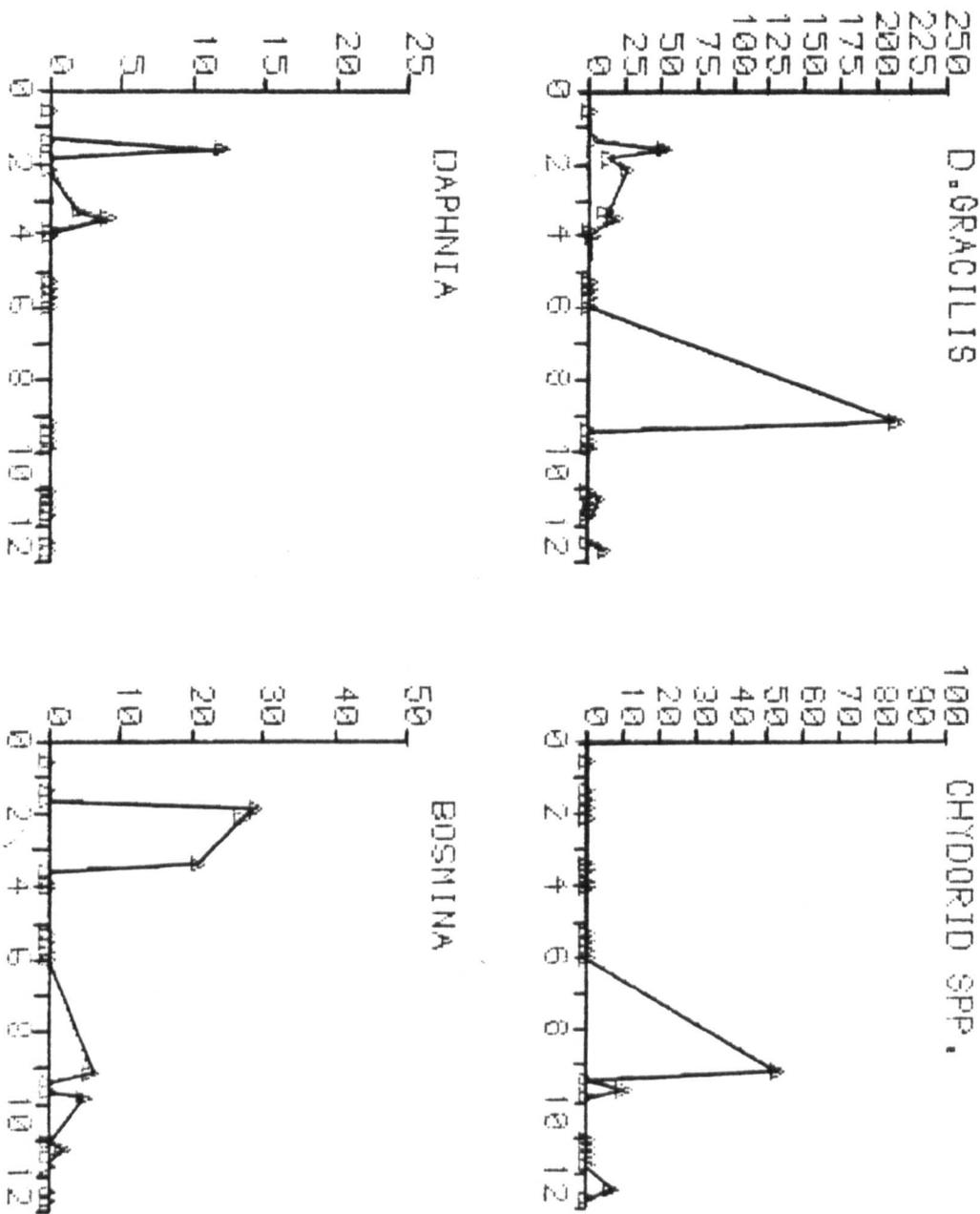


Figure c17 b: Annual abundance of freshwater taxa at South Alloa at low tide. Linear scales, Nos/m³

FRW DUNMORE HIGH TIDE

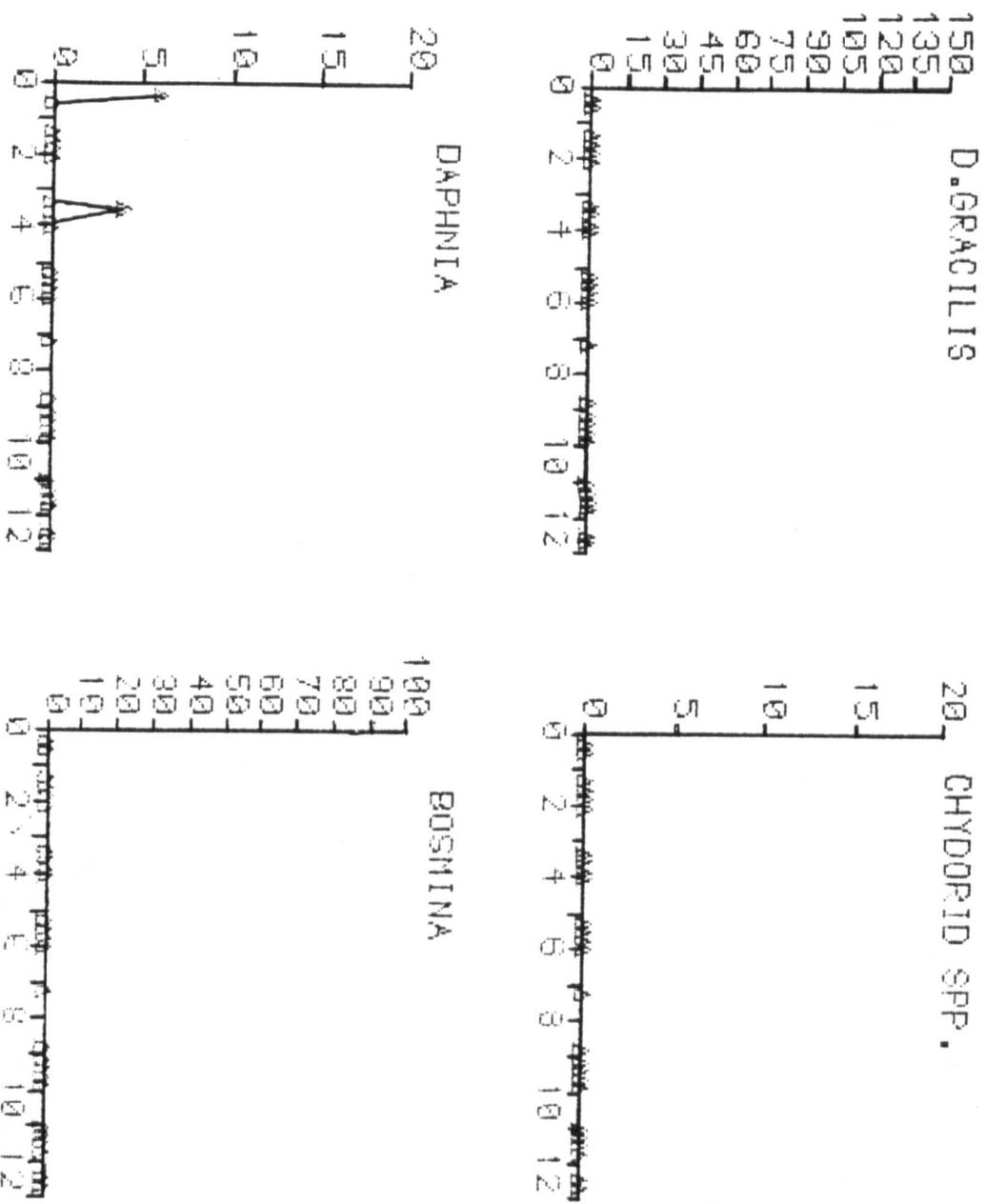


Figure C18 a: Annual abundance of freshwater taxa at Dunmore at high tide.
 Linear scales, Nos/m³

FRW DUNMORE LOW TIDE

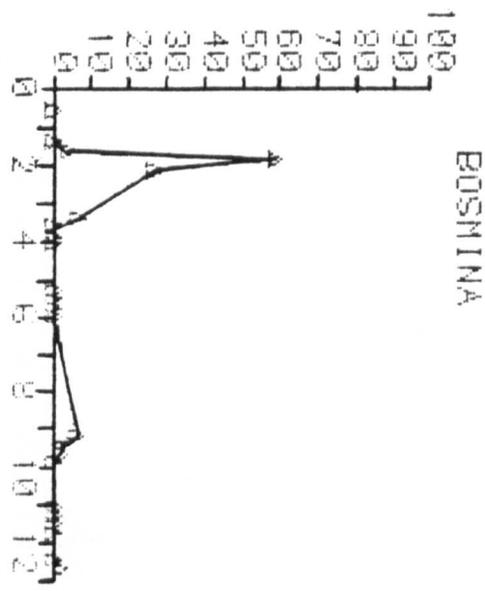
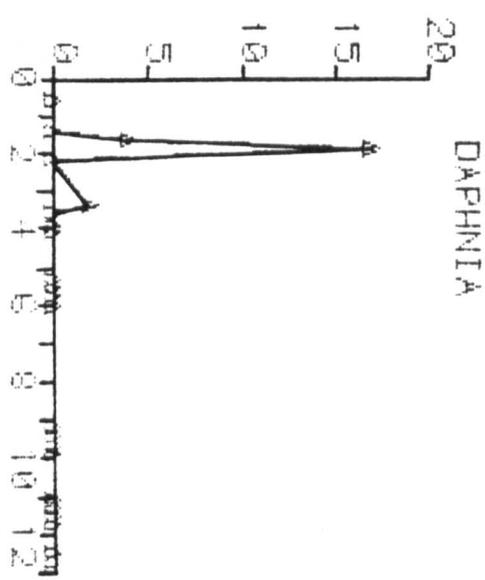
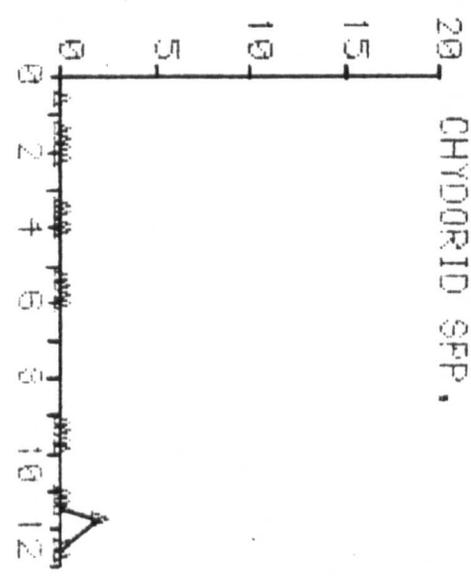
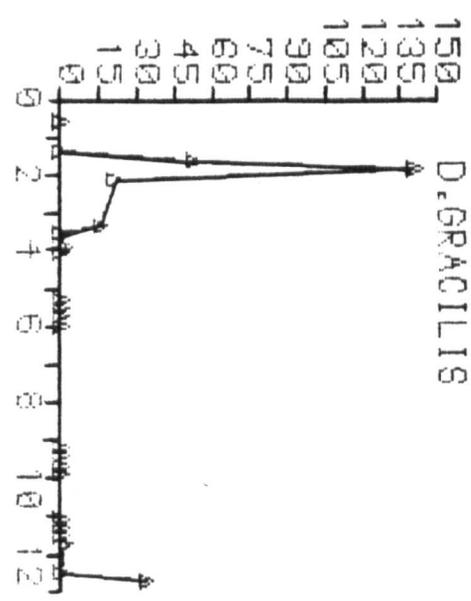


Figure C18 b: Annual abundance of freshwater taxa at Dunmore at low tide.
 Linear scales, Nos/m³

FRY KINCARDINE HIGH TIDE

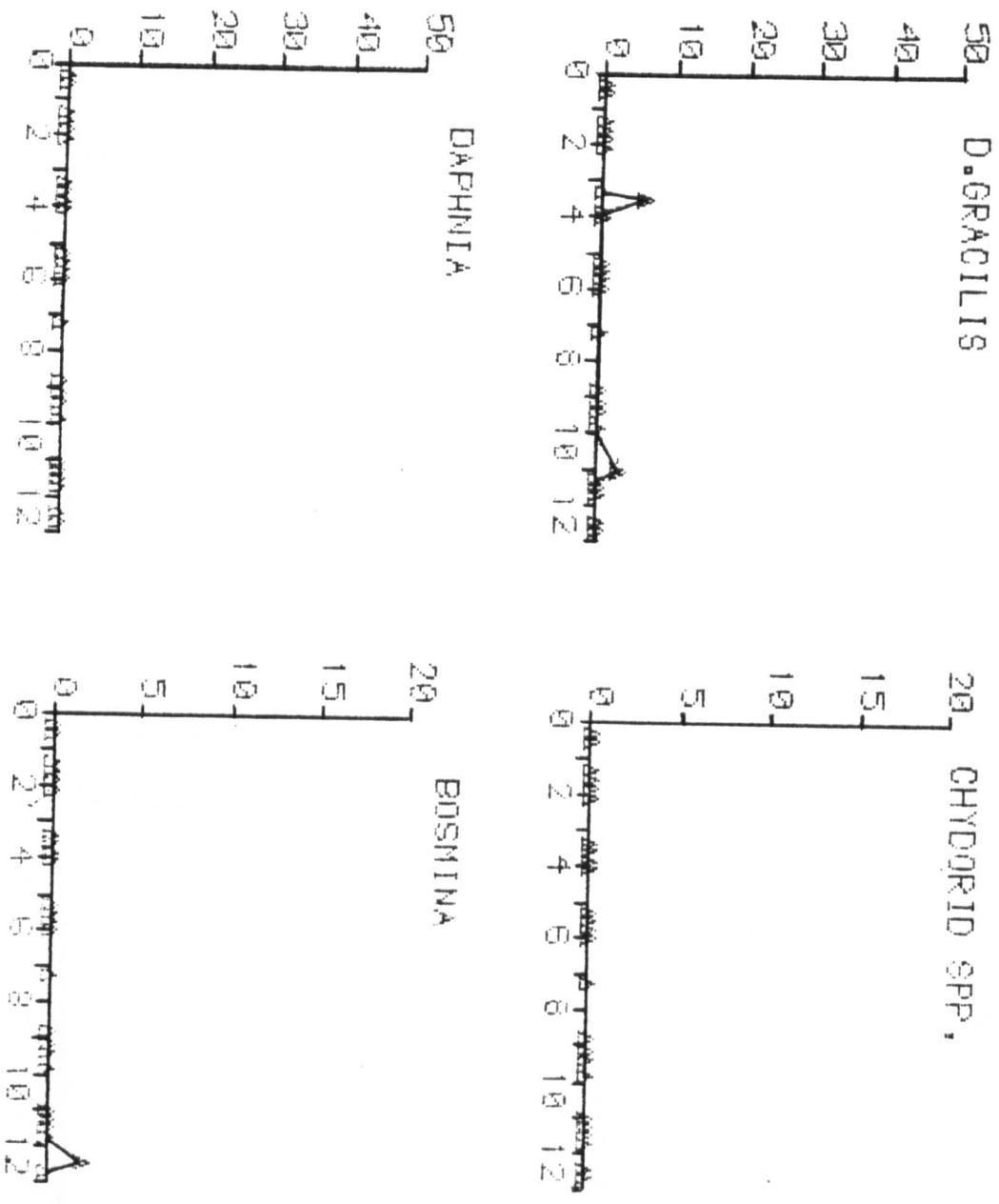


Figure C19 a: Annual abundance of freshwater taxa at Kincardine at high tide. Linear scales, Nos/m³

FRW KINCARDINE LOW TIDE

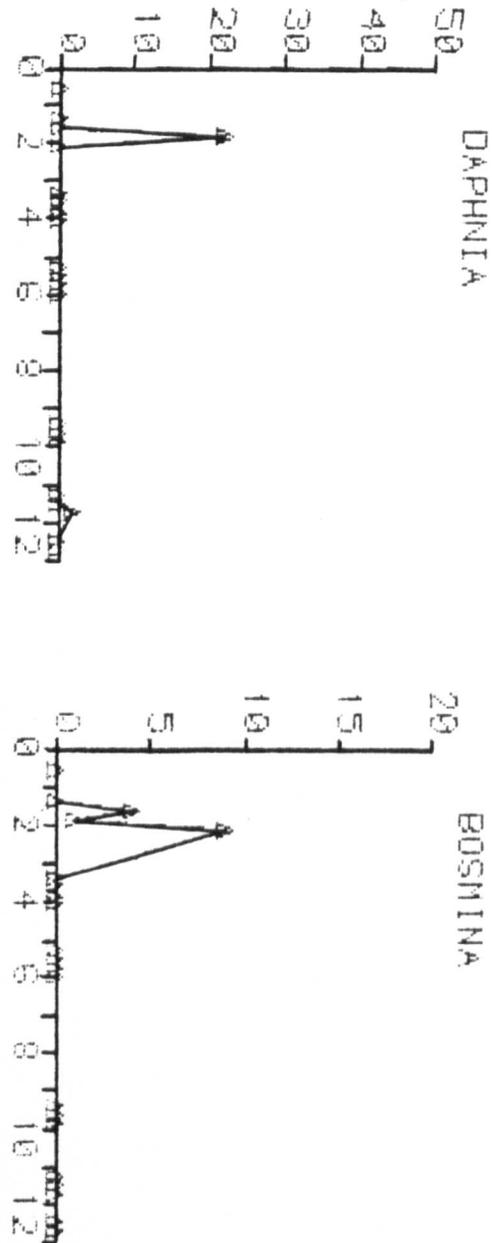
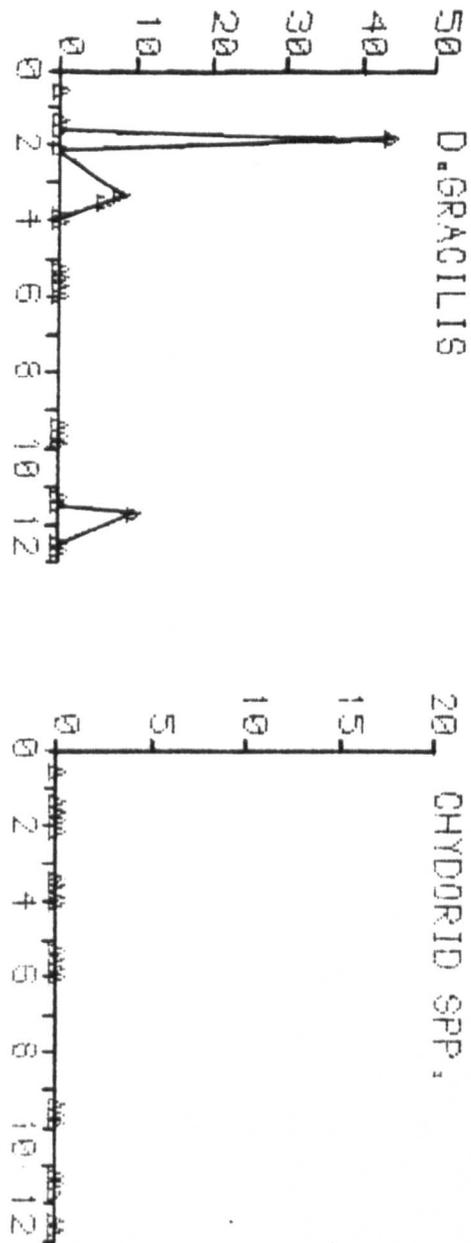


Figure C19 b: Annual abundance of freshwater taxa at Kincardine at low tide. Linear scales, Nos/m³