INVESTIGATIONS INTO ZOOPLANKTON ASSEMBLAGES OFF THE WEST COAST OF SCOTLAND

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For my Parents

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ABSTRACT

Zooplankton assemblages were examined from waters off the west coast of Scotland encompassing the Firths of Lorn and Clyde, the North Channel, and the Malin Shelf. Size fractionated samples (coarse, >1000μm; medium, 1000μm-330μm; fine, 330μm-180μm) were collected with a submersible pump from 10m and 30m depth in March (1987) and May (1986) providing a composite picture of the fauna in early and late spring conditions, respectively.

The feasibility of using image analysis as a method for processing zooplankton samples was examined. Although a programme was successfully operated to obtain individual measurement data, much work is still required before a fully automated programme for routine use by planktologists is available.

Total zooplankton numbers and biomass, and species distributions and relative abundances were examined. Species assemblages were identified using multivariate analyses. Biomass and abundance spectra by size were examined for the major station groupings. In general, meroplankton dominated the fauna in the Firth of Lorn while large numbers of *Calanus* spp. occurred in the Firth of Clyde. Small copepods such as *Oithona* spp. were characteristic of the assemblage on the Malin Shelf. Salinity, followed by temperature, showed the strongest association with the observed station clusters. Chlorophyll *a* and depth did not generally appear to influence station groupings.

The potential for the mixing and exchange of zooplankton between the regions of the study area was evaluated. The results suggest that zooplankton may be entrained from the Firth of Clyde by the Scottish Coastal Current during the spring period. The Malin Shelf may also be an important source of zooplankton for the Firth of Lorn during winter months when an onshore flow of Atlantic water occurs.

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1. INTRODUCTION

1.1 MIXING AND EXCHANGE PROCESSES

Mixing and exchange processes are of fundamental importance in the structure and maintenance of species assemblages within the marine environment (Zeitzschel 1982; Legendre and Demers 1984; Mackas *et al.* 1985; Greene and Wiebe 1990). Such processes can operate over a variety of spatial and temporal scales (Haury *et al.* 1978) ranging from major oceanic current systems (Bernal and McGowan 1981) to molecular diffusion processes (Okubo 1978). In all cases, these physical events play an important role, either directly or indirectly, in determining the distribution and abundance of planktonic material suspended in the water column (e.g. Steele 1978).

There are two types of processes which contribute to mixing in the oceans: advective and diffusive (Okubo 1978; Bonsell 1983). Advective processes are those which involve the large-scale vertical and/or horizontal movement of a water-mass including transport of the resident fauna (Okubo 1978). Diffusive processes involve a spatial exchange of material without any overall transport of water (Okubo 1978; Bonsell 1983). In general, advective processes are predictable events such as current and tidal regimes while diffusion is a random process occurring on a smaller spatial and temporal scale (Bonsell 1983). Diffusive effects are generally small relative to advective processes. 'Active diffusion' (Wolfenbarger 1975) can also occur through the interactions of motile organisms with local current regimes (see section 1.1.4.2).

1.1.1 Spatial and Temporal Scales

It is difficult to characterise mixing processes according to

their spatial and temporal scales. This is because many of the processes can occur at various locations along a time and space continuum. Although estimates of the spatial and temporal scales are provided for each of the processes discussed in the following section, they are only approximate.

Large-scale (> 1000km) advective processes in the worlds' oceans result from the combined effects of climatic patterns and wind stress (Pickard and Emery 1982). Major oceanic currents, such as the California Current, Gulf Stream Current and Kuroshio Current all occur within this category and are known to result in the large-scale horizontal transport of biogenic material. In the case of western boundary currents, such as the Gulf Stream and Kuroshio, the effect of the earths rotation, i.e. the Coriolis force, is of importance in determining the current flow (Pond and Pickard 1978) and also contributes to the formation of oceanic fronts (Harris 1986).

Many mixing processes occur as meso-scale events, i.e. in the order of 100 to 1000km and over a time period of weeks to months. This includes such diverse phenomena as coastal upwellings, eddies, and ocean fronts. These processes often occur in the coastal and continental shelf regions and can represent important sources of both horizontal and vertical mixing (Denman and Powell 1984). Haury *et al.* (1978) also include river plumes, island wakes, and seiches in their category of meso-scale processes although these are not discussed in any detail herein.

Upwelling events are associated with most of the eastern boundary currents, i.e. along the west coasts of major land masses, and often constitute regular seasonal phenomena (e.g. Dorman and Palmer 1981; Fraga 1981). The most common type of coastal upwelling is that which arises from winds which blow parallel to the coastline displacing surface water offshore through Ekman transport (Pickard and Emery 1982; Mackas *et al.* 1985). To compensate for the offshore flowing surface

layer, deep water is uplifted to the surface and transported shoreward (Harris 1986). This upwelled water is typically nutrient-rich, and derived from depths between 50 and 300m (Pickard and Emery 1982). Mackas *et al.* (1985) also describe upwelling events which derive from the interactions between seasonal average currents and submarine canyons, as well as the propagation of continental shelf waves.

The term 'eddies' is generally used as a catch-all to include a variety of meso-scale events such as meandering and filamenting of major current systems, semi-attached and isolated ring currents, planetary waves and others (Robinson 1983). One particular type of eddy which has been well studied is the formation of rings, typically associated with fast-moving western boundary currents. Such rings can represent an important source of water exchange for the adjacent offshore and continental shelf regions (Smith 1978; Haury *et al.* 1978; Richardson 1983; Denman and Powell 1984). In the Gulf Stream, meanders which break away from the main current path form either warm-core rings in the Slope Water region (e.g. Richardson 1983; Wiebe and McDougall 1986) or cold-core rings in the Sargasso Sea (e.g. Wiebe, 1976; Wiebe and Boyd 1978). Rings may be as large as 200-300km in diameter, with an average life span of 1 year for cold-core rings and 6 months for warm-core rings (Richardson 1983). These phenomena are not restricted to the Gulf Stream region, but have also been observed off Australia (e.g. Cresswell and Golding 1980; Cresswell and Legeckis 1986; Tranter *et al.* 1986), in the Kuroshio Current (e.g. Kawamura *et al.* 1986; Nagata *et al.* 1986; Yamamoto and Nishizawa 1986), and off the Oregon coast (Moum and Caldwell 1988).

Oceanic fronts, and shelf-break fronts can also constitute meso-scale phenomena and are important regions of vertical mixing (Mackas *et al.* 1985). Oceanic fronts may occur at the edges of impinged eddies, or at the boundaries of large current systems (Mackas *et al.* 1985). Vertical mixing at these locations may occur as a result of both strong

vertical and horizontal current shears (Lutjeharms *et al.* 1985). Shelf-break fronts occur along the edge of the continental shelf at the boundary between the colder, fresher water on the shelf and the warmer, more saline oceanic waters (Denman and Powell 1984; Harris 1986). These frontal systems are sites of exchange between different water masses (e.g Gatien 1976) and mixing may be further enhanced through tidally-forced instabilities (Herman and Denman 1979) and wind forcing events (Harris 1986).

Processes occurring on a spatial scale of 10 to 100km and a temporal scale lasting from days to weeks, can be categorised as coarse-scale events. Examples are internal tides, tidal fronts and wind-induced mixing, although other events such as upwelling, and shelf-break fronts can also occur along these spatial and temporal scales.

Tidal mixing and tidal fronts are prime mechanisms for vertical mixing in coastal waters (Le Fèvre 1986). Semi-diurnal tides can generate sufficient turbulent mixing through interaction with an irregular bottom topography to prevent the formation of a thermocline or halocline and maintain the water column well mixed (Denman and Powell 1984). It is this tidal energy which gives rise to the fronts which occur at the boundaries between mixed and stratified waters (Simpson 1981). Several models have been developed to predict the occurrence of tidal fronts (Simpson and Hunter 1974; Fearnhead 1975; Simpson 1976; Pingree and Griffiths 1978) incorporating parameters such as tidal velocity and water column depth, the degree of surface-layer stratification and bottom friction. Typically, a tidal front will occur during the summer when a seasonal thermocline is present, although in regions of high fresh water outflow the front may also represent a salinity gradient (e.g. McKay *et al.* 1986; Edwards *et al.* 1986). The spatial scale of the fronts will be determined by the local bathymetric features.

Wind-induced vertical mixing refers to mixing in the surface layer

of the ocean as a direct result of a wind stress at the air/water interface. The greater the wind speeds, the greater the energy at the interface which is mixed downward throughout the water column reducing the degree of stratification. Wind induced vertical mixing, combined with seasonal cooling in the surface layer, is an important component in the breakdown of the seasonal thermocline in temperate waters (e.g. Raymont 1963).

At the fine end of the spectrum, operating on scales of millimetres to metres and seconds to hours, are small-scale processes such as vertical shears, internal waves, Langmuir cells, salt fingers and diffusion (see Haury *et al.* 1978). Mixing processes resulting from these fine-scale events are of particular importance in determining the small scale distributions of nutrients and plankton assemblages (e.g. Mitchell *et al.* 1985; Lazier and Mann 1989).

Vertical shear refers to the differential motion which occurs at water boundaries, or the interface between layers of different density within the water column (e.g Fischer *et al.* 1979; Svendsen 1986). The source of the energy typically derives from wind and the differential movement of one layer relative to another results in vertical shear. Water from the deeper layer can be entrained by the higher-velocity surface layer and internal waves generated along this interface can break and result in mixing across the boundary (Bonsell 1983).

Langmuir cells are small circulatory currents which can range in size from a few centimetres to 10m in diameter and result from the interaction of wind and waves at the water surface (Barstow 1983; Harris 1986). Much work has been devoted to the study of these cells and how they affect the distributions of plankton assemblages (e.g. Fedoryako 1982; Hamner and Schneider 1986; Zohary and Robarts 1989).

The remaining processes, i.e. salt fingers and diffusion, are representative of very fine-scale mixing processes. An example of this type of mixing is double diffusion which occurs due to the differential

molecular diffusion rates of heat and salt within a water column (Pond and Pickard 1978). Diffusive processes may represent an important source of small-scale mixing in the oceans on a scale of one to several metres (Pond and Pickard 1978).

1.1.2 Seasonal Events

In addition to the mixing events discussed above, the formation and dissipation of a seasonal thermocline and/or halocline is an important process which determines rates of vertical mixing in the surface layer of the water column (e.g Wickstead 1965). In temperate waters, wind-induced vertical mixing combined with surface cooling results in a deepening of the surface-mixed layer during the winter months (Holligan and Groom 1986). In the spring, increased solar radiation, often accompanied by freshwater runoff, decreases the density of the surface layer leading to the formation of a seasonal pycnocline (e.g. Elliott and Clarke 1991). While this feature persists, water exchange between the near-surface and deep-water layers is greatly restricted and as the season progresses nutrients in the surface-layer become depleted and phytoplankton growth limited (Tett 1987). Storms, turbulent mixing due to internal waves, and tidal mixing can all enhance mixing across the boundary between the two layers (e.g. Walsh *et al.* 1978; Holligan *et al.* 1985; Geyer and Farmer 1989). In the autumn, decreased surface heating combined with strong winds eventually leads to the dissipation of the pycnocline and deepening of the mixed layer (e.g Raymont 1963).

1.1.3 Types of Materials Exchanged

Any material dissolved or suspended in the water column can be exchanged through mixing processes (e.g. Darnell and Soniat 1979). This

includes conservative physical properties such as heat and salt (Pond and Pickard 1982), chemical properties including oxygen, dissolved organic and inorganic nutrients (e.g. Darnell and Soniat 1979; Tett and Edwards 1984), particulate organic material (e.g. Hansell *et al.* 1989), as well as plankton (e.g Fraser 1937, 1939, 1952; Russell 1935, 1939; Yoder and Ishimaru 1989) and nekton (e.g. Olson and Backus 1985). There is also some evidence that bottom sediments may be transported through processes such as internal waves (Southard and Cacchione 1972; Winant 1974), downwelling events (Figueiras and Pazos 1991) or tidal regimes (Shu *et al.* 1990).

Materials may be exchanged either through horizontal advection or vertical mixing. In the case of dissolved inorganic and organic nutrients, the breakdown of the seasonal pycnocline, as discussed above, is a major mechanism for the vertical exchange of nutrients between the deep and surface layers (e.g. Tett and Edwards 1984). The horizontal advection of nutrients can also occur as the result of freshwater outflow from river systems (Solórzano and Grantham 1975; Malone 1976) which can represent an important source of nutrients in coastal waters (Burrell 1988). Entrainment of water in the outflowing surface layer of an estuary or fjord can also constitute an important mechanism for the mixing of nutrients from deeper waters into the surface layer (e.g Sinclair *et al.* 1981; Harrison *et al.* 1991). Meso-scale processes occurring in the open ocean can facilitate the exchange of nutrients. The large-scale advection of nutrients by the California Current has been recognized as an important factor contributing to high levels of production off the California coast (Bernal and McGowan 1981). Impinging eddies can provide an influx of nutrients into adjacent regions (e.g. Smith 1978; Paffenhöfer *et al.* 1980) while nutrients can also be entrained into the ring edge or upwelled at the centre (Gould and Fryxell 1988). Fournier *et al.* (1977) suggested that the sporadic advection of Slope Water onto the adjacent Scotian Shelf could account

for 20% of the nutrients required by phytoplankton during the spring and summer.

Plankton suspended within the water column is carried along passively by the water currents and the exchange of both phytoplankton and zooplankton between different regions is well documented. Strong surface winds may advect phytoplankton populations from one region to another through Ekman transport (Fraga *et al.* 1988; Erga 1989; Figueiras and Fraga 1990). Advection may also be important in the transport of phytoplankton biomass (e.g. Falkowski *et al.* 1988, Walsh 1988; Yoder and Ishimaru 1989) and phytodetritus (Hansell *et al.* 1989) from continental shelf waters into the adjacent continental slope and oceanic regions.

Within the water column, lateral dispersion can be accomplished through vertical shear and turbulent diffusion (Okubo 1978) and tidal advection (Cloern *et al.* 1989; Cochlan *et al.* 1990). At the water/sediment interface the resuspension of resting cysts through closed circulation cells (e.g. Figueiras and Pazos 1991) may represent an important mechanism of vertical mixing. Much effort has been directed towards developing models which predict the effects of mixing processes on phytoplankton assemblages within the surface mixed layer (e.g. Tett and Edwards 1984; Kamykowski 1990).

Steele (1978) stated that the greater an individuals' body size, the greater its independence from water movements and mixing processes. Zooplankton, though still passive components of the water column, do exhibit a much higher degree of motility than phytoplankton (e.g Longhurst 1976a). The consequences of fine-scale mixing processes may therefore be less pronounced for zooplankton then for phytoplankton assemblages. Larger-scale advective and mixing processes such as current systems (e.g. Blackburn 1979; Bernal and McGowan 1981; Roesler and Chelton 1987; Lindley *et al.* 1990), impinging eddies (Wiebe *et al.* 1976; Haury 1984), and upwelling events (Arcos 1981; Smith *et al.* 1981; Locke and Corey 1989), can all result in the vertical and/or horizontal

advection and mixing of zooplankton assemblages. Surface currents can horizontally transport zooplankton assemblages (e.g. Gardner 1982), in some cases providing an important means of dispersal (Locke and Corey 1989). Lindley and Hunt (1989) found that advection by currents was important in the recruitment of two neritic copepod species in the North Atlantic Ocean and North Sea. Tidal excursions and deep-water renewal processes in fjords can also horizontally transport zooplankton faunas across fjord sills (e.g. Fosshagen 1980; De Ladurantaye *et al.* 1984; Lewis and Thomas 1986; Aksnes *et al.* 1989). Vertical mixing can also result in fine-scale variability in microzooplankton distributions within the water column (Incze *et al.* 1990).

Fish, with their relatively large body size and increased motility are even less influenced by mixing and exchange processes than zooplankton and phytoplankton. However, their distributions and abundances can still be influenced directly by larger-scale physical processes (e.g. Olson and Backus 1985). In addition, the eggs and larval stages of many species are directly affected by the same processes acting on the plankton assemblages and this has been shown to greatly affect recruitment success (e.g. Bailey 1981; Norcross and Shaw 1984; Incze *et al.* 1989). This also holds true for the planktonic stages of many benthic organisms (e.g. Banse 1986).

1.1.4 Conditions which may Enhance or Reduce Mixing Processes

1.1.4.1 Physical Parameters

Physical features such as the coastline direction (Denman and Powell 1984), and bathymetry (Steele 1978; Freeland and Denman 1982; Mackas *et al.* 1985), islands (Simpson *et al.* 1982) and variable processes such as tidal currents (Pingree and Griffiths 1978; New and Pingree 1990; Maze and Le Tareau 1990), freshwater outflow (Sutcliff *et*

al. 1976; Smetacek 1986) and strong winds (Tett and Edwards 1984) all represent factors which may act to enhance local mixing conditions.

Factors which reduce the potential for vertical mixing and exchange include the input of heat and freshwater which both decrease the surface density and therefore increase stability of the water column (Tett and Edwards 1984). The development of a seasonal pycnocline can lead to isolation of the deep-water mass and under certain conditions, (e.g. in fjords with restricted water exchange) anoxic conditions may develop (e.g. Lindahl and Hernroth 1983; Edler 1984). Water depth can also affect mixing potential as the greater the depth the greater the energy required to mix the water column. In the specialized case of fjords, sill and basin depths are also of importance in determining the frequency and extent to which deep water renewal occurs (Gade and Edwards 1980).

1.1.4.2 Biological Processes

There is considerable evidence to suggest that planktonic organisms, through vertical migrations, are able to favourably alter their position within the water column in order to exploit differential current regimes (e.g. Peterson *et al.* 1979; Anderson and Stolzenbach 1985; Kaartvedt 1989). This phenomenon was referred to as 'active' dispersion by Wolfenbarger (1975) indicating that the mixing process had been accomplished using energy supplied by the organism itself; this differed from 'passive' diffusion where the mixing energy was supplied by physical processes.

'Active' diffusion in phytoplankton appears limited to dinoflagellates capable of undertaking diel vertical migrations (e.g. Seliger *et al.* 1970; Heaney and Talling 1980; Tyler and Seliger 1981; Anderson and Stolzenbach 1985). This ability to alter their distribution within the water column in order to minimise advective losses (e.g.

Anderson and Stolzenbach 1985) may well contribute to their bloom forming potential.

For zooplankton, the advantages of selectively utilising differential current regimes (e.g. Hardy 1936, 1953) appears to be species retention, either within a localized area such as a fjord or estuary (e.g. Wooldridge and Erasmus 1980; Kaartvedt 1989), or within a larger geographical region (e.g. Peterson *et al.* 1979). Kaartvedt (1989) concluded that without selective positioning within the water column to avoid advective losses, mysids within a Norwegian fjord would be unable to maintain local populations. This resulted in a severe selection pressure for the development of behavioral patterns to enhance retention (Kaartvedt 1989). Within a system, individuals may also exploit currents to undertake small-scale horizontal excursions (Wooldridge and Erasmus 1980). On a larger scale, Peterson *et al.* (1979) described how several copepod species, through ontogenetic migrations, were able to maintain populations in coastal waters off Oregon characterised by upwelling processes and a pronounced frontal zone.

Retention mechanisms can also be utilised by larval stages of some benthic species (e.g. Cronin and Forward 1986). Some species, through selective positioning within the water column (e.g. Rothlisberg 1982; Le Fèvre and Bourget 1991), also appear able to exploit differential current regimes in order to enhance dispersion.

1.1.5 The Importance of Mixing and Exchange Processes

From a biological perspective, the importance of mixing and exchange processes is in the maintenance or enhancement of productivity. For phytoplankton assemblages, this can be achieved either indirectly through an influx of nutrients or directly through the advection of new material. Turbulent diffusion of nitrate across a thermocline can help to maintain production levels in nutrient-limited phytoplankton

populations (Tett and Edwards 1984). Larger-scale processes, such as upwellings, transport large volumes of nutrient-rich water resulting in enhanced levels of primary production (see Richards 1981; Suess and Thiede 1983). Vertical mixing is also important in maintaining large, non-motile phytoplankton cells (e.g. diatoms) within the euphotic zone (Margalef 1978).

Increases in phytoplankton biomass are not always the result of increased productivity. Ortner *et al.* (1984) suggested that a redistribution of zooplankton caused by deepening of the vertical mixed layer may have contributed to increased phytoplankton and bacterioplankton standing stocks within a Gulf Loop intrusion. Similarly, Heywood and Priddle (1987) concluded that shallow eddies may have partially isolated phytoplankton assemblages thereby reducing grazing pressure. Increased standing stocks may also result through advection or physical processes which act to locally aggregate phytoplankton cells (e.g. Olson and Backus 1985; Le Fèvre 1986; Legendre and Le Fèvre 1989).

Zooplankton assemblages do not respond directly to mixing processes, but advection can result in a significant increase to the local biomass within a definable area. Cox and Wiebe (1979) estimated that advection by warm-core eddies could account for between 8 and 16% of zooplankton populations in the mid-Atlantic Bight. Roman *et al.* (1985) found that intrusions of shelf/slope water in a Gulf Stream warm-core ring resulted in a 5-fold increase in zooplankton biomass between the sizes of 64 to 333µm and a 3-fold increase in the >333µm fraction. Although, on the longer-term, the high biomass levels were maintained by *in-situ* production, the intrusions may have represented a seeding mechanism for establishing new species within a ring. Coyle *et al.* (1990) found that the biomass of zooplankton within Auke Bay, Alaska, could be substantially increased through the advection of adult *Calanus marshallae*, *Metridia ochotensis*, and copepodids of *Neocalanus plumchrus* from outside the bay.

However, not all mixing and exchange processes are beneficial for planktonic assemblages, or for the ecosystem. Extensive vertical mixing can result in phytoplankton being mixed out of the surface layer and below the 'critical depth', i.e. the point in the water column where the average daily level of irradiation is sufficient for photosynthesis to equal respiration (Riley 1942; Sverdrup 1952). High volumes of freshwater runoff or tidal mixing can dilute populations of phytoplankton and zooplankton maintaining localised low levels of standing stock (e.g. Sinclair *et al.* 1981; Gowen *et al.* 1983; Jones and Gowen 1985). Advection and horizontal turbulent diffusion can also have a negative effect on the recruitment success of larval stages of benthic organisms (e.g. Hill 1990) and larval fish (e.g Bailey 1981; Incze *et al.* 1989).

It has also been suggested that the formation of toxic algal blooms may result from the advection of offshore waters containing 'seed' populations to inshore waters where conditions are favourable for a bloom to develop (e.g. Fraga *et al.* 1988; Erga 1989). Recent work has shown that downwelling (Figueiras and Pazos 1991) and upwelling (Pitcher 1990) events may also contribute to the formation of algal blooms through the resuspension of resting cysts of the bloom forming species. In all cases, it would appear that mixing processes are of great importance in the development of toxic blooms.

1.1.6 Fjord/Continental Shelf Systems

Fjord ecosystems (e.g. Matthews and Heimdal 1980; Eilertsen and Taasen 1984; Syvitski *et al.* 1987) and the contiguous continental shelves (e.g. Hennemuth 1975; Barnett and Jahn 1987) have long been regarded as areas of high biological productivity. Recently, it has been suggested that these increased levels of productivity may be due to an exchange of material between the two areas (Syvitski *et al.* 1987).

Denman and Powell (1984) suggest that the dominant physical forces acting in coastal areas are horizontal advection by ocean currents and estuarine circulation patterns. The importance of freshwater outflow in determining rates of exchange between fjord and shelf areas is now recognized (see Skreslet 1986*a*), particularly how this affects the functioning of Coastal Currents (e.g. Simpson and Hill 1986). Variability in the volume of freshwater discharged can influence recruitment success in fishes (Bugden *et al.* 1982; Skreslet 1983, 1986*b*) through fluctuations in primary production. However, recent work, (e.g. Sinclair *et al.* 1986), has suggested that advective processes can directly affect the early life-history stages of zooplankton and fish populations and need not be channelled through primary producers.

A fjord may be a net exporter or importer of material depending upon levels of productivity inside and outside the fjord, and on the nature and frequency of water exchange (Syvitski *et al.* 1987). Significant portions of the phytoplankton production within a fjord may be exported to confluent coastal waters (e.g. Platt and Conover 1971; Lewis and Platt 1982) where primary production is further enhanced through the input of nutrient-rich deep-water entrained in the outflowing surface layer (Stockner *et al.* 1977, 1979; Sinclair *et al.* 1986). The spring bloom often begins earlier in fjordic waters due to increased water column stability (e.g. Braarud 1974) which may result from freshwater runoff (Tett and Wallis 1978). Fjords are also potential sites for sustaining high levels of primary production throughout the summer because of nutrient inputs derived either through entrainment or riverine inflow (Syvitski *et al.* 1987).

The exchange of zooplankton between fjords and coastal waters is also known to occur (e.g. Sands 1980; Skreslet 1983; Cooney 1986; Kaartvedt *et al.* 1988) and can represent an important source of organic material for both ecosystems. Skreslet (1983) maintained that deep, Norwegian fjords acted as overwintering and spawning grounds for

copepods, such as *Calanus finmarchicus*, whose nauplii were subsequently advected out of the fjords where they comprised a major food item for cod larvae.

The effect of advective processes are not unidirectional; Sands (1980) concluded that several species of chaetognaths in Korsfjorden, Norway, were advected into the fjord by the near-surface currents, during deep-water renewal. Cooney (1986) found that the onshore transport of copepods into Alaskan fjords from coastal waters represented an important source of energy for the fjord ecosystems. Similarly, Stockner *et. al.* (1977, 1979) observed that phytoplankton biomass was advected from outside waters into Howe Sound where biomass levels were reduced due to turbidity. Regardless of the net-direction of transport, the exchange of material between fjords and coastal waters is an important process in which energy is transferred between two semi-isolated ecosystems. Syvitski *et al.* (1987) recommended that future work in this area should focus on determining in what form and under what conditions organisms are transported from coastal waters into fjord ecosystems. Clearly the reverse process is of equal importance.

1.2 AUTOMATED METHODS FOR PROCESSING MARINE PLANKTON

To understand the structure and dynamics of marine ecosystems requires, in addition to knowledge regarding species composition and abundance, information regarding size structure and biomass within the faunal assemblage. The collection of these data is often very tedious and time consuming and new methodology is continually being sought to improve data acquisition. In recent years much progress has been made towards the automation of sample processing - but generally not without compromise.

Early work in this area produced automated particle counting devices such as the Coulter Counter (Sheldon and Parsons 1967*a*) and the

Hiac (Pugh 1976). The Coulter Counter, initially used in medical research, measured the charge of a particle passing through an electrical field and converted this to an equivalent spherical diameter. Adapted for use in marine science, it enabled the examination of detailed size spectra for particulate material suspended in seawater over a wide range of sizes (Sheldon and Parson 1967*b*; Sheldon *et al.* 1972). The Hiac was a particle counting device for use with phytoplankton and microzooplankton (1-900μm equivalent spherical diameter; Pugh 1976). It operated on the basic principle that light attenuation by a particle passing through a collimated light beam was related to its projected area (Pugh 1976). Both these techniques suffered from two main disadvantages: 1) the incapability to distinguish between living and detrital material, and 2) the lack of taxonomic information for individual particles comprising the spectrum (Haury *et al.* 1978). In addition, because particle size was expressed as equivalent spherical volume, lengths of long, thin particles were often underestimated (Rolke and Lenz 1984). The problem of taxonomic information has partially been solved through the recent use of flow cytometry (e.g. Yentsch *et al.* 1983, 1986; Cunningham and Leftly, 1986).

In addition to the particle-counting devices, various computer-based techniques for counting and/or sizing planktonic material were also developed. Cunningham and Purewal (1983) described a micro-computer connected to several keyboards with programmable, user-defined keys. This system saved time associated with manually recording species abundances but only provided for the recording of numerical data.

A similar device was developed by Jackson *et al.* (1984). In this setup an Utermohl's inverted microscope was attached to a personal computer, again with pre-defined keys. This system differed from that of Cunningham and Purewal (1983) in that it allowed individuals to be both enumerated and sized. For both the above systems, the main time-saving advantage was in not having to manually record on paper, or enter

subsequently into a computer for analysis, the data collected.

Another automated method for processing plankton samples used speech recognition (Williams and Briton 1986). In this method a voice activated key-board was attached to an IBM PC and a pre-defined species vocabulary programmed into the computer. During sample processing the scientist's voice was translated by the keyboard electronics into the appropriate numerical code. This procedure was found to halve sample processing time, while allowing an experienced taxonomist to identify and stage individual plankters. However, it did not provide any information regarding the size structure or biomass of the fauna.

Most attention towards the automation of sample processing has recently focused on the use of image analysis. Image analysis is a powerful computer technique which operates on spatially oriented data and can provide information on both the abundance and size of individual particles. However the real power of image analysis lies in its potential use for pattern recognition, i.e. the automated identification of objects on the basis of statistical parameters relating to their morphometry (Uhlmann *et al.* 1978; Jeffries *et al.* 1980, 1984; Dietrich and Uhlig 1984; Tsuji and Nishikawa 1984; Gorsky *et al.* 1989; Estep and MacIntyre 1989), density (Jensen 1986) or even texture (Ekstrom 1984; Langford *et al.* 1986). It is this ultimate goal which has maintained a continued interest in the development of image analysis extending to the present day.

1.2.1 Image Analysis

1.2.1.1 General Principles

Image analysis can be defined as the quantification and classification of images and of objects of interest within images (Joyce-Loebl 1985). In any programme there is a set protocol which

includes: 1) image capture 2) enhancement 3) segmentation, 4) identification, and 5) measurement. A brief review of the more salient features of image analysis is presented below. This emphasises the object-oriented use of image analysis, similar to that used in the present study.

1) Image capture:

An image is a two-dimensional distribution of energy (Joyce-Loebl 1985). Most images are comprised of energy in the visible light spectrum although other sources, such as x-rays, acoustic waves, and even nuclear particles can be utilised (Joyce-Loebl 1985). The most common method for entering images is with a standard television camera. During the process an image is converted to an electronic signal which is quantised with respect to both its spatial coordinates and its energy (Gonzalez and Wintz 1977). The resulting digitised image is comprised of a matrix of spatially ordered picture elements known as pixels (Lillesand and Kiefer 1979) and the energy, or intensity, at any given pixel represented by a "grey value" (Joyce-Loebl 1985). The range of possible grey values, known as the grey scale, will vary among instruments although scales of 0 to 63 (i.e. 2^6 bits) or 0 to 255 (i.e. 2^8 bits) are most common (Joyce-Loebl 1985). Values at the low end of the grey scale (i.e. 0) represent black while the upper limit (i.e. 255) represents white. Image quality is influenced by both the size of the image matrix and the range of the grey scale. Gonzalez and Wintz (1977) recommend a minimum matrix size of 256^2 pixels and 64 grey levels for image analysis work.

2) Enhancement:

Once a digitised image has been obtained there are an endless number of functions which can be used to improve the image display prior to analysis. It should be emphasised, however, that no amount of enhancement can compensate for a poor image quality resulting from improper illumination or focusing at the time of capture (Joyce-Loebl 1985). Much processing time can be saved by ensuring that these

parameters are optimal before beginning the programme.

Enhancement functions are often used for one of the following purposes: i) shading corrections, ii) to improve the contrast between objects of interest and the background, or iii) to improve resolution at boundary interfaces and reduce the signal to noise ratio.

i) During image capture the transformation of energy into grey values may vary among pixels even under constant light conditions, an effect known as shading (Kontron 1985). If left uncorrected this effect can result in problems at the time of object discrimination (discussed below) because similar objects will have different grey levels depending on their location within the image. Clearly, when illumination levels vary across an image, the problem can be quite serious.

Several functions are available to correct for shading (Kontron 1986). One such method involves adjusting the original image using a value obtained from a suitable reference image. For example, for an image displaying dark objects against a light background a sheet of white paper could be used as a reference image. Once entered, the reference image is subjected to a median filter to reduce camera noise and the average overall grey value determined. This grey value can then be added to all pixels in the original image to adjust for illumination errors at the time of image capture.

ii) Functions in the second category include those which alter the distribution of grey levels within an image. Often when an image is captured, a noisy signal will result in the objects of interest occupying only a small portion of the total grey scale (Kontron 1986). With this group of functions it is possible to isolate the portion of the grey scale of interest and expand the values to cover the total available range. The result is enhanced contrast between objects of interest and the background.

iii) The third category is comprised of digital image filters. Filtering can be performed either in the frequency domain by means of

transformations or in the spatial domain by means of convolution (Jensen 1986). As only spatial operating filters were used in the present study several of the more common types are discussed below. For more details regarding filters in the frequency domain (e.g. Fourier analysis) consult Castleman (1979).

Spatial filters, such as low- and high-pass filters, transform the grey value of a pixel according to a function which takes into account the neighbouring pixel values within a predefined matrix (Jensen 1986). Such transformations are often known as convolutions and may be linear or non-linear functions (Joyce-Loebl 1985). In linear operations each pixel is replaced by the average value of the neighbouring pixels within the matrix (Joyce-Loebl 1985). In non-linear functions each pixel is replaced by the average grey level value only if it differs from its neighbour by a set value (Joyce-Loebl 1985).

Low-pass filters are a type of linear filter used to reduce random noise within the high frequency components of an image (Ekstrom 1984). One problem with this type of filter, however, is the blurring of edges and details within an image; the degree of blurring will be proportional to the size of the matrix over which the grey values are averaged (Gonzalez and Wintz 1977).

A non-linear median filter, however, will reduce random noise while maintaining features of interest, such as edges (Kontron 1985). For the median filter, the grey value of the pixel being processed is replaced by the median value of the pixels within the selected matrix. This allows for better definition within the image (Ekstrom 1984).

The high-pass filter is also commonly used. This enhances the high-frequency components of an image while reducing the low-frequency signal (Joyce-Loebl 1985). High-pass filters are useful in the enhancement of edge features within an image and to reduce blurring (Ekstrom 1984).

With all filters it is important to select the appropriate matrix

size, in relation to the features of interest within the image, in order to obtain the best results.

3) Segmentation

Segmentation is the step in image analysis where objects of interest for subsequent measurement are discriminated from other objects and/or the background. There are three main methods of segmentation: 1) thresholding (also referred to as discrimination or detection; Kontron 1985) 2) edge finding, and 3) region growing (Joyce-Loebl 1985). In all cases the resulting image is binary with all objects of interest displayed as white (grey value = 255) and all else displayed as black (grey value = 0). This contrasts with the previous steps in the program where an image has been comprised by a range of grey values.

Thresholding is the simplest method available for discriminating objects of interest (Joyce-Loebl 1985; Kontron 1985). This involves setting an upper and a lower grey value such that all pixels falling within the boundaries comprise objects of interest and are set to white, and those falling outside the boundaries are set to black. Thresholding depends on similar objects having comparable grey values throughout the image. If not, the objects will not be equally discriminated by the same set of boundary conditions which can lead to serious measurement errors.

Edge-finding and region-growing techniques are gradient based methods of discrimination (Castleman 1979). They are more commonly applied to remote sensing or aerial data where the objective is not so much to distinguish between individual objects displayed against a relatively uniform background, but to identify regions of interest from a mosaic of information. Edge-finding techniques operate by assuming that areas of rapidly changing grey values will correspond with boundaries between regions of interest (Joyce-Loebl 1985). Similarly, region-growing operates on the principle that pixels having similar grey values belong to a common area of interest. Boundary lines are then erected between dissimilar regions within the image (Joyce-Loebl 1985).

4) Identification

The identification function must be used before any object specific measurements can be made. This does not apply to chord or field specific measurements (discussed below) because these are global and pertain to all regions of interest (Kontron 1985). In this step of the programme, the boundaries of individual objects are identified using either fourfold or eightfold connectivity (Joyce-Loebl 1985). Simply put, starting from an initial outer pixel, the logical status of the neighbouring pixels is determined in either four or eight vector directions. The outermost white pixels (i.e. pixels of interest in the binary image) are then connected to form a chain which delimits the outer boundary of an individual object. Once objects are identified in this manner, each individual object is displayed in a different colour. This enables checking to ensure that individual objects are not touching, i.e. if they are touching they will display the same color and be measured as one object.

5) Measurement

Several types of measurements may be made using image analysis. These include field, chord, densitometric and object measurements (Kontron 1985).

Object measurements are made on individual objects within an image, following discrimination and identification. Many different types of measurements can be made, some of the more common being length, width, area and perimeter. Since each measurement is per individual object this also indirectly provides a count of the objects within the image. The number of objects can also be obtained independent of the measurement parameters.

Field parameters provide a measurement relating to the combined properties of all objects within the image; for example, the field area measurement provides one value for the total area of all objects within the image.

Densitometric measurements are those relating to the specific grey values of individual pixels (Fawell 1976). The Lambert-Beer law states that light absorption is directly proportional to the mass concentration of the absorbing substance. Therefore, using image analysis it is possible to measure the quantity of a particular substance in an image on the basis of its grey values (Kontron 1985).

Chord analysis was often used in early image analysers when the available memory was insufficient to store an entire image and the image was processed line by line (Joyce-Loebl 1985). Using this lined grid, the lengths of 'detected chords' (i.e. within the object, as opposed to undetected chords in the background; Joyce-Loebl 1985) could be used to obtain information about the size, shape and orientation of an object. However, most modern image analysis systems do not generally use chord measurements (Joyce-Loebl 1985).

Of course, prior to any measurement programme, a suitable scale must be entered into the system relating pixels to the units to be used for the measurement parameters. In the case of object-specific measurements, this is most often accomplished using an eyepiece micrometer.

Most image analysis programmes also include some facilities for processing data acquired by the system. This often includes statistical analysis of the measurement data and graphical presentation of results as frequency distributions. The analysis and display facilities available vary considerably among machines.

Finally, pattern recognition may be incorporated into the image analysis programme. Pattern recognition allows objects to be classified into categories on the basis of certain criteria derived from initial measurements of representative individuals (Uhlmann *et al.* 1978). Pattern recognition, although generally recognised as the ultimate goal of automated image analysis, is not routinely incorporated into many image analysis programmes.

The above section has provided a brief review of some of the major components of image analysis, however it is by no means complete. For a full discourse on image analysis the reader should consult the comprehensive manual prepared by Joyce-Loebl (1985). Numerous books on the general principles of digital image processing are also available (e.g. Jensen 1986; Ekstrom 1984; Gonzalez and Wintz 1977).

1.2.1.2 Previous Applications

Applications of image analysis can be divided into two broad categories. The first contains those which examine large scale spatially ordered data sets such as those obtained through remote sensing instruments or aerial photography. The second category contains applications where interest is focused at the level of the individual or particle. Much information regarding large-scale physical and biological properties in the oceans has been obtained through remotely sensed data (e.g. the Coastal Zone Color Scanner; Aarup 1990; Kuring *et al.* 1990). However, the acquisition, image processing and associated problems, of these data are quite different to those techniques used in obtaining object-specific measurements. Since the use of image analysis in the present study was object oriented, this section is limited to a review of literature pertinent only to this area of image analysis. For information on image analysis techniques relating to remotely sensed data, several comprehensive texts are available including Hord (1982), Jensen (1986), and Muller (1988).

The application of object-oriented image analysis is not new. Since the early 1950's (Estep *et al.* 1986) the technique has had a variety of diverse applications both in industry and medicine (e.g. Watson 1952; Ingram and Preston 1970; Pettipher and Rodrigues 1982). Application of image analysis to marine planktonic material dates back to the 1970's (Fawell 1976). In the intervening time, the technique has

been used in the examination of zooplankton (Jeffries *et al.* 1980, 1981, 1984; Dietrich and Uhlig 1984; Rolke and Lenz 1984; Mills and Confer 1986) and phytoplankton (Uhlmann *et al.* 1978; Tsuji and Nishikawa 1981, 1984; Furuya 1982; Estep *et al.* 1986; Estep and MacIntyre 1989; Gorsky *et al.* 1989) assemblages, fish eggs (Asano and Tanaka 1984), bacteria (Sieracki *et al.* 1985; Bjørnsen 1986; Thomsen 1991), flocculent particles (Eisma *et al.* 1990), and energy reserves in calanoid copepods (Arts and Evans 1991). These studies differ greatly in the degree to which image analysis techniques are employed, including the use of pattern recognition. There is also considerable variability in systems used and the types of material examined.

In its simplest form, image analysis has merely been used to provide a spatially digitized image which could then be measured using a light-pen, or similar such device (Lough and Potter 1983; Mills and Confer 1986; Arts and Evans 1991). None of these studies included image enhancement or segmentation techniques, and no pattern recognition was incorporated into the programme. All were interactively operated.

A number of studies have utilized more extensive image analysis techniques but without incorporating pattern recognition (e.g. Furuya 1982; Rolke and Lenz 1984; Sieracki 1985; Bjørnsen 1986; Estep *et al.* 1986; Eisma *et al.* 1990). These studies incorporated automatic enhancement, segmentation and measurement procedures, often with an operator present to interactively remove unwanted particles, separate adjoining particles or adjust threshold grey values for discrimination.

The final group of studies consists of those incorporating pattern recognition into the programme, and has included studies on both phytoplankton (Uhlmann *et al.* 1978; Tsuji and Nishikawa 1984; Estep and MacIntyre 1989; Gorsky *et al.* 1989) and zooplankton (Fawell 1976; Jeffries *et al.* 1980; Dietrich and Uhlig 1984; Jeffries *et al.* 1984).

Attempts to classify phytoplankton taxa using pattern recognition have had considerable success. Uhlmann *et al.* (1978) required only 15

individuals to obtain sufficient morphometric data to distinguish between five different phytoplankton genera, although they were of distinctly different shapes. Tsuji and Nishikawa (1984) were able to distinguish between three dinoflagellate species on the basis of cell length, area and perimeter, and a Fourier descriptor. Estep and MacIntyre (1989) successfully distinguished between three dinoflagellates and a diatom species on the basis of their aspect ratio, cell length, width and area; there was, however, some region of overlap among the species where operator intervention would be required for identification.

Application of pattern recognition to marine zooplankton has allowed differentiation between species which are morphometrically distinct (Fawell 1976) and between major taxonomic groups (Jeffries *et al.* 1980; 1984). Fawell (1976) used a function based on area and perimeter to distinguish among a mixed assemblage containing a copepod, a chaetognath and a euphausiid. Jeffries *et al.* (1980) used simple morphometric parameters to classify zooplankton according to major taxonomic groups (e.g. copepods, fish eggs, fish larvae, cladocerans, chaetognaths, euphausiids) with a 93% accuracy level. In a later study (Jeffries *et al.* 1984), the classification criteria were considerably expanded to include morphometric, invariant moment functions and Fourier descriptors. Although the accuracy attained was only 90% the difference could be attributed to the use of preserved material as opposed to paper silhouettes which were used in the original work.

In the above zooplankton studies, the level of classification was only to broad taxonomic groupings. Dietrich and Uhlig (1984) used pattern recognition to distinguish between the 6 naupliar and copepodid stages of the harpacticoid copepod *Tisbe holothuriae*. Using morphometrics they were able to identify the various developmental stages, although problems were encountered in distinguishing between young females without egg sacs and adult males due to the similarity in

form and size.

1.3 OBJECTIVES

The first main objective of this study was to conduct a detailed investigation of zooplankton assemblages in waters off the west coast of Scotland. The study area stretched from approximately 54 to 57°N and 4 to 9°W, encompassing the Firths of Lorn and Clyde, the Malin Shelf and parts of the North Channel. Although previous investigations of the fauna within the study region had been conducted, much of the work was of a localised nature. In addition to covering a small area, relative to the present investigation, many of the previous studies were concerned with only one species, (e.g. *Calanus finmarchicus*, Nicholls 1933*a* and *b*; Marshall 1933; Marshall *et al.* 1934), or broader taxonomic groups (e.g. barnacles, Barnes 1956; euphausiids, Mauchline 1960). The present study provided an opportunity to examine the zooplankton fauna within this large spatial area on two occasions: May 1986 and March 1987. Together, these two cruises provided a composite picture of the zooplankton fauna in what can be regarded as pre- and post-spring bloom conditions. For this reason, reference is made to the March cruise prior to the May cruise throughout the text.

Within this framework, the specific objectives of this aspect of the project were as follows:

1) To examine the variation in total numbers and biomass of zooplankton throughout the study area, within and between cruises, and how these were partitioned within different size fractions.

2) To examine the species composition and distribution of zooplankton at the time of each cruise.

3) To examine species relationships throughout the study area using multivariate techniques in order to identify faunal groups. To examine in detail the species contributing to each group, and determine

if faunal groups could be related to physical factors such as temperature, salinity and depth, or biological factors such as phytoplankton biomass.

4) To examine biomass partitioning among species within each of the groups identified using the multivariate techniques to determine possible differences in the structuring of the faunal assemblages relating to energy flow through the system.

5) To use these results to evaluate the potential for the mixing and exchange of fauna to occur between the fjord and coastal waters, and to examine how this may vary between the two firths given differences in their local hydrography. The implications this may have for production at higher trophic levels is also discussed.

The second main objective of the study was to investigate the feasibility of using image analysis as a method for the routine processing of zooplankton samples. For this purpose an image analysis programme to provide measurement data for individual zooplankton was developed. Experiments were conducted in order to select a length measurement for use in the present study and the results were compared with those obtained using conventional microscopy methods. In addition, experiments were conducted to examine various aspects of the machine's performance, including the following:

1) The role of magnification as a source of variability in individual length measurements.

2) A comparison of size frequency distributions obtained using the image analyser and conventional microscopy methods.

3) Examination of the variability in discrimination parameters among individuals within selected copepod taxa.

4) A comparison of projected surface area measurements for selected copepod taxa based on prosome length and total body length.

2. STUDY AREA

The study area was located off the west coast of Scotland between the longitudes of approximately 54°30′ and 56°30′N and the latitudes of 4°30′ and 8°30′W. The total area of investigation was approximately 8.4 x $10^3 km^2$ and contained four prime regions of interest: 1) the North Channel, 2) the Firth of Clyde, 3) the Firth of Lorn, and 4) the Malin Shelf (Figure 2.1). In this section a general description, and a review of the physical and biological properties of the study area are presented; this includes data collected at the time of the two cruises examined in the present study. The emphasis is placed on regional, rather than local, events as these are the processes believed to be most relevant to the present investigation.

2.1 BOTTOM TOPOGRAPHY AND BATHYMETRY

The North Channel is the deepest bathymetric feature in the study area (Figure 2.2). The main body of the channel is delineated by the 100m contour and the average channel depth lies between 120 and 140m (Howarth 1982). Maximum depths of about 315m are found in a deep trough of water which lies along the eastern side of the Channel just west of the Rhins of Galloway on the Scottish coast. To the northwest, a sill at approximately 40m located between Islay and Malin Head demarcates the northern limits of the channel (Howarth 1982).

Exchange of water between the Firth of Clyde and the North Channel is restricted by the presence of the Great Plateau located in the outer region of the Firth of Clyde (Figure 2.2). The plateau extends over an area of approximately $810 km^2$ and has an average water depth of about 44m (Mill 1892). Landward of the Great Plateau is the main channel of the

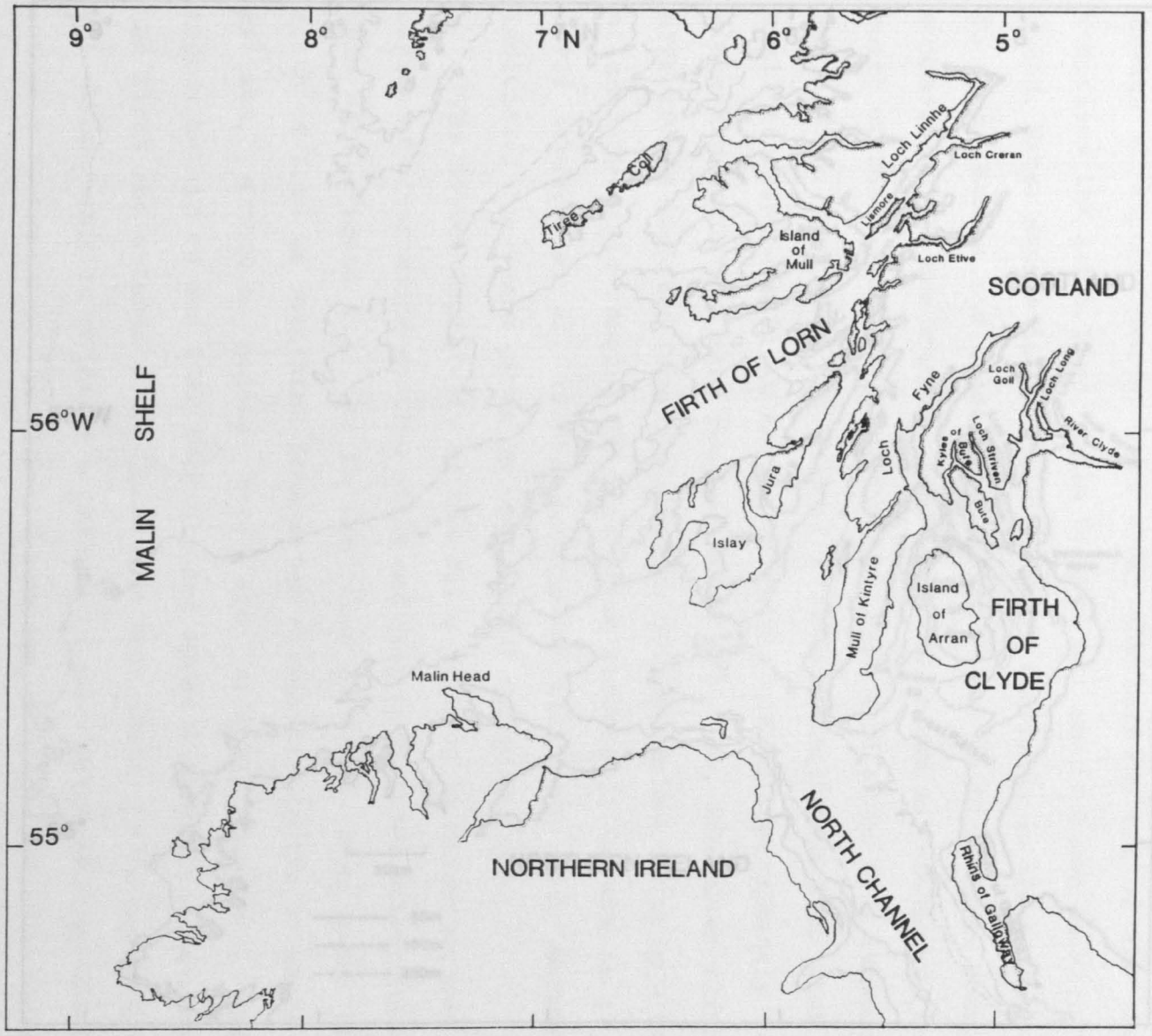


Figure 2.1 Chart showing the study area located off the west coast of Scotland.

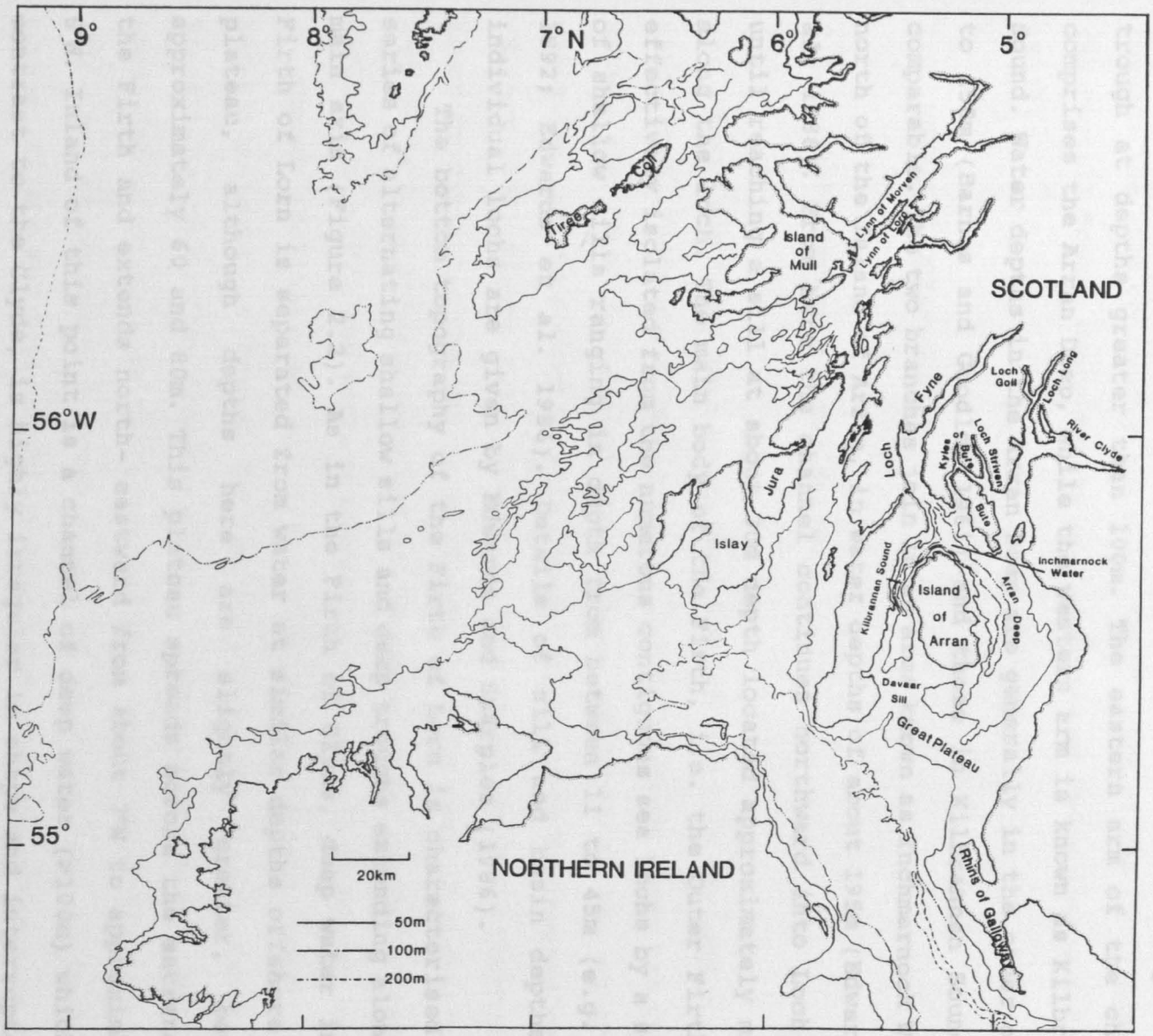


Figure 2.2 Chart showing bathymetry in the region of the study area located off the west coast of Scotland.

Outer Firth. This channel circumscribes all but the southwestern corner of the Island of Arran where its path is broken by the Davaar Sill, at a depth of about 40m (Edwards *et al.* 1986). The main body of the channel is enclosed within the 50m contour, although there is a deep central trough at depths greater than 100m. The eastern arm of the channel comprises the Arran Deep, while the western arm is known as Kilbrannan Sound. Water depths in the Arran Deep are generally in the order of 130 to 150m (Barnes and Goodley 1961) and those in Kilbrannan Sound are comparable. The two branches join in an area known as Inchmarnock Water, north of the Island of Arran, in water depths of about 195m (Edwards *et al.* 1986). From here the channel continues northward into Loch Fyne until reaching a sill at about 30m depth located approximately midway along the loch. The main body of the Firth, i.e. the Outer Firth, is effectively isolated from the numerous contiguous sea lochs by a series of shallow sills ranging in depth from between 11 to 45m (e.g. Mill 1892; Edwards *et al.* 1986). Details of sill and basin depths for individual lochs are given by Edwards and Sharples (1986).

The bottom topography of the Firth of Lorn is characterised by a series of alternating shallow sills and deep troughs extending along its main axis (Figure 2.2). As in the Firth of Clyde, deep water in the Firth of Lorn is separated from water at similar depths offshore by a plateau, although depths here are slightly greater, between approximately 60 and 80m. This plateau spreads across the entrance of the Firth and extends north- eastward from about 7°W to approximately 6°W. Inland of this point is a channel of deep water (>100m) which, in contrast to the Clyde, is highly irregular in shape and interrupted by numerous shoals. Pockets of deep water up to 250m can occur in this region. This channel continues inland until reaching the island of Lismore where shallow sills to the southwest and northeast of the island (~30m and 5m, respectively) separate the Lynn of Morvern to the west, from the Lynn of Lorn to the east. Depths in the Lynn of Lorn are

relatively shallow and typically less than 50m. West of Lismore in the Lynn of Morvern, depths mostly exceed 60m with isolated deeps of 100m or greater.

Westward from the Firth of Lorn, water depths gradually increase towards the 200m contour on the Malin Shelf. West of the shelf edge lies the Rockall Trough where depths are in excess of 2000m (Lee and Ramster 1981).

2.2 PHYSICAL OCEANOGRAPHY

2.2.1 Characteristic Water Masses

There are three main water masses which occur in the region of the study area. These are Atlantic water, Irish Sea-Clyde water and Coastal water; the first two derive from sources external to the study area while the last is formed locally through mixing with freshwater run-off (Ellett 1979; Figure 2.3). Atlantic water is of oceanic origin and is found primarily in the region of the Malin shelf west of approximately 8°W. It is a relatively warm and saline water mass, characterised by a salinity of >35°/$_{oo}$ and surface temperatures above 8°C in winter and 13°C in summer (McKinley *et al.* 1981; Ellett and Edwards 1983). Irish Sea-Clyde water is formed by the mixing of Irish Sea water (S = 32-34°/$_{oo}$) with outflow from the Firth of Clyde (McKay *et al.* 1986). The resulting water mass is characterised by a salinity of between 34 and 35°/$_{oo}$ and temperatures between 7 and 8°C in winter and 12 to 13°C in summer (Ellett and Edwards 1983). This water mass forms the core of the Scottish Coastal Current which is transported, via the North Channel, along the west coast of Scotland (Simpson and Hill 1986). The Coastal water mass, which is formed locally, occurs primarily inshore in the vicinity of the Firths of Lorn and Clyde where freshwater run-off is high (McKinley *et al.* 1981). It is characterised by low salinities

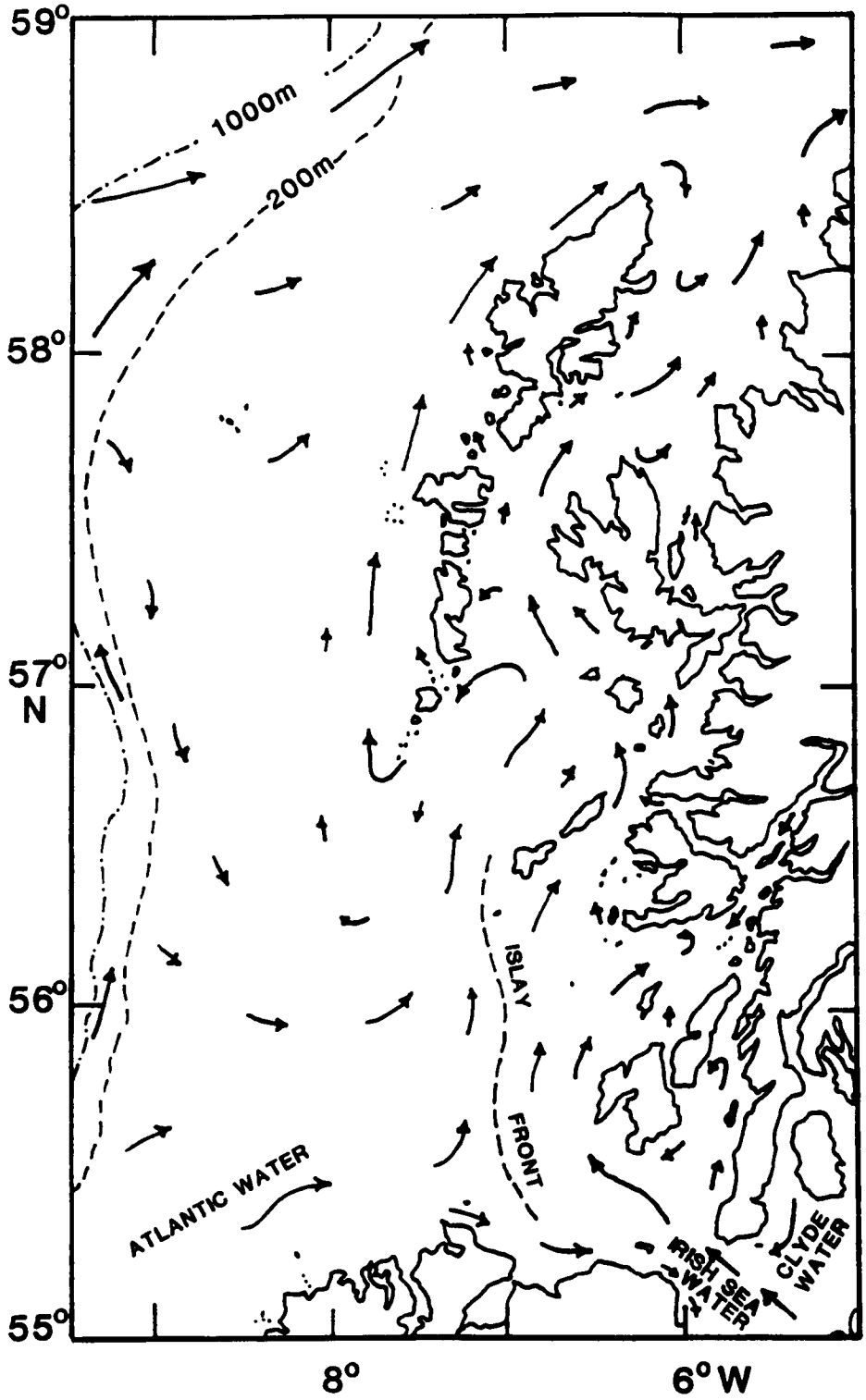


Figure 2.3 Surface circulation off the west coast of Scotland during summer. Modified from Ellett (1979).

<33°/₀₀ (Ellett and Edwards 1983), with the salinity at any given time reflecting the mixing ratio of freshwater. Temperatures of this water mass exhibit marked seasonal variability.

2.2.2 Seasonal Variations in Water Properties

Throughout some regions of the study area the water column is continually well mixed due to the combination of shallow depths, a strong tidal current and an irregular bottom topography (e.g. Ellett and Edwards 1983; Edwards *et al.* 1986; Simpson and Hill 1986). In these areas, which include most of the North Channel and the Firth of Lorn, surface conditions are generally representative of those throughout the entire water column. Stratification occurs only in regions of greater water depths where tidal mixing is weaker and cannot overturn the less dense surface water which occurs either through heating and/or freshwater run-off. This occurs primarily on the Malin Shelf, in the deep waters of the Firth of Lorn and in the Firth of Clyde and in these areas a seasonal thermocline and/or halocline typically develops (Ellett 1979; Grantham et al. 1983*a*; Edwards *et al.* 1986).

Craig (1959) described the seasonal pattern for temperature in the region off the west coast of Scotland. Surface temperatures throughout the area typically exhibit a winter minimum and a late summer maximum and bottom waters in well-mixed areas generally follow the same trend. However, on the Malin Shelf (Ellett 1978; Ellett and Edwards 1983), in the Firth of Clyde (Edwards *et al.* 1986) and in certain regions of the Firth of Lorn (Grantham *et al.* 1983*a*) a summer thermocline develops and water below the thermocline remains cooler. On the Malin Shelf, a cool, lower salinity water mass appears to be formed *in situ* during the winter months (Edelsten *et al.* 1976) and by late spring, bottom temperatures may be as much as 2 C° (i.e. <8°C) less than those above the thermocline (>10.5°C; Ellett 1978). In the Outer Clyde, deep-water renewal by Irish

Sea water occurs over the Great Plateau between autumn and spring, and during summer this water becomes isolated beneath a thermocline and halocline (Edwards *et al.* 1986). Bottom temperatures are therefore dependent on both the timing and magnitude of the renewal processes and the properties of the external water mass. Typical surface and bottom temperatures in the Outer Firth during winter are 7.2 to 7.6°C and 7.5 to 8.5°C, respectively, and in summer, 12 to 13°C and 8.5 to 10°C, respectively (Edwards *et al.* 1986). In the North Channel, a tidal current in excess of about 1.5ms^{-1} results in a generally homogeneous water column, although weak stratification may occur during summer in the deeper waters off the Rhins of Galloway (Edwards *et al.* 1986). In winter, temperatures in the Channel are typically around 7.0°C while summer temperatures are slightly warmer, around 12 to 13°C (Craig 1959). Finally, in the Firth of Lorn, temperatures are virtually isothermal, between about 6.5 and 7.5°C, throughout the water column in February, even to depths of >200m (Grantham 1983; Grantham *et al.* 1983*b*). In summer pockets of slightly cooler water (~11.4°C) occur below 125m underlying warmer surface layers of about 12.5°C (Grantham *et al.* 1983*a*). The relatively small temperature differential from surface to bottom suggests frequent mixing of the water column.

The seasonal distribution of surface salinity throughout much of the study area shows a pattern similar to temperature; only in the shelf region is there some deviation (Craig 1959). In the coastal waters, surface salinities are greatly affected by the volume of freshwater run-off which, along the west coast of Scotland, exhibits a winter maximum (Admiralty 1974; Ellett and Edwards 1983). Correspondingly, surface salinities are therefore at a minimum in coastal waters during this period. In the Firth of Clyde, the high volume of freshwater outflow during the winter creates a halocline at a depth of about 50m (Edwards *et al.* 1986) which contributes to the maintenance of the Great Plateau front (see section 2.2.3 below). Surface salinities at this time range

from 32.5 to 33.5 °/∞ increasing towards the mouth of the fjord (Edwards *et al.* 1986; Matthews 1987). Below the halocline they are generally higher (≥ 34.4°/∞; Matthews 1987), reflecting the pulsed winter inflow of denser, more saline bottom water over the Great Plateau (Edwards *et al.* 1986). Seasonal fluctuations in the volume of freshwater run-off from the Clyde can depress salinities in the Coastal Current by as much as 0.15°/∞ (Ellett and Edwards 1983). This is evident in the North Channel where in winter, salinities range from between approximately 33.5 to just over 34°/∞ (Edwards *et al.* 1986; Matthews 1987). In the Firth of Lorn, surface salinities in February were not below 33°/∞ in 1982 and 32°/∞ in 1983 (Grantham 1983; Grantham *et al.* 1983*b*) although low salinity water (≤ 24°/∞) was present further inland in Loch Linnhe on both occasions. Grantham (1983) suggests that most freshwater outflow in the Firth of Lorn is diverted through the deeper passage of the Sound of Mull to the west of Lismore island. This would account for the relatively high surface salinities observed near the mouth of the firth at this time. However, it is also possible that much of the freshwater run-off is diluted through vertical mixing as it proceeds towards the mouth of the firth. Deep water in the Firth of Lorn is derived from the North Channel and a deep, inflowing layer of dense, saline water (≥ 34°/∞) was observed during both years (Grantham 1983; Grantham *et al.* 1983*b*). The degree to which this bottom water progresses into the firth appears to be related to variations in the local weather pattern (Grantham *et al.* 1983*b*).

In summer, surface salinities in the coastal water are generally higher due to reduced freshwater outflow (Milne 1972). In the Firth of Clyde, surface salinities are higher than those observed in winter by up to 0.5°/∞ (Edwards *et al.* 1986), while in water below the thermocline salinities may be slightly higher (>33°/∞) due to reduced mixing (Jones 1986). In the North Channel salinities are also increased with values generally between 34 and 34.2°/∞ (Edwards *et al.* 1986). The 34°/∞

isohaline used to delineate the Scottish Coastal Current often extends eastward onto the Great Plateau at the mouth of the Clyde, indicative of the increased volume of the current and the reduced freshwater outflow from the Clyde at this time. In the Firth of Lorn, Grantham *et al.* (1983*a*) found no evidence in July 1982 of an out-flowing freshwater surface layer in the region between the islands of Lismore and Colonsay. There was, however, good evidence of mixing, with salinity values, even at depths >200m, ranging between 33.6 and 33.8°/∞ (Grantham *et al.* 1983*a*).

In contrast to the coastal waters, surface salinities offshore generally exhibit a summer minimum and a winter maximum (Craig 1959), with little seasonal difference in the deep-water properties (Craig 1959; Lee and Ramster 1981). In winter, surface salinities on the Malin Shelf are typically high with the 35°/∞ isohaline extending eastward of 8°W, and more saline water, the maximum near 35.3°/∞, at depth (Craig 1959). However, in summer salinities are generally decreased and the 35°/∞ isohaline retreats to the west of 8°W (Lee and Ramster 1981); this generally occurs to the North of the Islay Front (McKay *et al.* 1986). The general decrease in salinity is attributed to the spread of lower salinity Coastal Current water over the thermally stratified shelf water (Ellett and Edwards 1983; McKay *et al.* 1986). The extent to which this lower salinity water extends onto the shelf is subject to considerable inter-annual variability (McKinley *et al.* 1986).

2.2.3 Frontal Regions

The term 'front' is used to characterise the boundary which occurs at the meeting of two distinct water masses (Fearnhead 1975). Such a boundary also often delineates between a well-mixed and a stratified water mass (e.g. Jones *et al.* 1984). Several fronts exist in the waters off the west coast of Scotland, their occurrence initially predicted on

theoretical grounds by Fearnhead (1975) and by Pingree and Griffiths (1978). Two of these are directly relevant to the present study: the Islay Front, located to the west of Islay, and the Great Plateau front, located at the entrance to the Firth of Clyde. A third front located in the Sound of Jura has been previously investigated by Jones *et al.* (1984).

The Islay front is a persistent late spring-autumn feature off the west coast of Islay and marks the transition between the well-mixed waters of the Coastal Current and the thermally stratified Atlantic water on the Malin Shelf (Figure 2.3; Becker 1973; Ellett 1978; McKay *et al.* 1986). The front also represents a marked salinity gradient between the two water masses; McKay *et al.* (1986) found evidence of the front in both distributions of salinity and ^{137}Cs, but not in temperature in May, when the temperature differential between offshore and onshore waters was minimal. It is thought that the strong salinity gradient between the two water masses acts to enhance the stability of the frontal system (Simpson *et al.* 1979; Ellett and Edwards 1983). The position of the front is generally centred about a longitude of 7°W, although this may vary (Economides *et al.* 1985). Previous work by Simpson *et al.* (1979) has shown the front to be of biological importance.

The Great Plateau front is located at the entrance to the Firth of Clyde and marks the boundary between the well-mixed waters of the North Channel and the stratified waters in the Outer Clyde (e.g. Figure 2.8b; Edwards *et al.* 1986). It is a permanent feature of the region, maintained through surface heating during the summer and freshwater runoff during the winter (Edwards *et al.* 1986). The front is manifest primarily as a surface feature and exhibits some variability in its position near the mouth of the Clyde (Edwards *et al.* 1986).

2.2.4 Current Patterns

Much of our knowledge regarding the circulation of waters off the west coast of Scotland has been acquired over the last twenty years through studies examining the dispersal patterns and mixing ratios of radioactive caesium (^{137}Cs and ^{134}Cs) discharged from the Windscale nuclear fuel reprocessing plant located in Cumbria (e.g. Jefferies *et al.* 1973; Mauchline 1980; Livingston *et al.* 1981; McKinley *et al.* 1981; Jefferies *et al.* 1982; McKay and Baxter 1985; Economides *et al.* 1985; McKay *et al.* 1986). To a large degree, the current view reflects that proposed earlier by Craig (1959) and Barnes and Goodley (1961) although the flow of Coastal Current water through the Outer Hebrides has been further clarified (McKay *et al.* 1986).

The circulation of surface waters in the vicinity of the study area can briefly be summarised as follows. There is a persistent northward flow of water from the Irish Sea through the North Channel which is augmented by outflow from the Firth of Clyde to form the Scottish Coastal Current (e.g. Ellett *et al.* 1984; Figure 2.3). This current flows north along the east coast of Scotland, primarily wind driven (Howarth 1982; Economides *et al.* 1985) but reinforced by buoyant freshwater outflow (Simpson and Hill 1986). The mean speed of the Coastal Current has been estimated at about $5 km d^{-1}$ (Simpson and Hill 1986) with a volume transport through the North Channel in July 1981 of $4.7 \times 10^{4} m^{3} s^{-1}$ (McKay *et al.* 1986). Both speed and volume exhibit considerable inter-annual variability as was evident during the anomalous conditions of 1976 (e.g. McKinley *et al.* 1981). At this time, the Coastal Current spread out across the Sea of the Hebrides as a coastal plume with low salinities extending well onto the Malin Shelf (see also Jefferies *et al.* 1982).

At the mouth of the North Channel (i.e. northwest of the Kintyre Peninsula) there is some evidence that the Coastal Current may, at

times, reverse flow back into the channel along the Irish coast (Economides *et al.* 1985). In addition, there is usually an inflow of Atlantic Water along the western side of the channel, although this is variable (e.g. Craig and Slinn 1957; Craig 1959; Ellett and Edwards 1983; Economides *et al.* 1985). As the current leaves the North Channel it encounters the Atlantic water mass at the Islay Front where mixing between the two water masses is minimal (Ellett 1979). Most of the Coastal Current passes northward through the Tiree Passage off the west coast of Mull to reach the Small Isles (McKay *et al.* 1986). Here, the tidal current is reduced and mixing occurs between the two water masses with most of the flow continuing north through the Little Minch east of the Outer Hebrides and a smaller component to the west of the islands (McKay *et al.* 1986). Flow rates outside the North Channel are lower, in the order of 2 to 3kmd^{-1} for the Sea of the Hebrides (Ellett and Edwards 1983; Economides *et al.* 1985). East of the Islay Front, part of the Coastal Current flows onshore where it comprises the deep, saline water mass in the Firth of Lorn (see Grantham 1983; Grantham *et al.* 1983*b*). On the Malin Shelf, flows are generally weak, in a north and eastward direction (Ellett and Edwards 1983). During the winter, mixing may result in an increased onshore penetration of Atlantic water (McKinley *et al.* 1981) although during summer this is limited by the presence of the Islay Front.

In the Firth of Clyde, the surface current is highly influenced by the prevailing winds (Barnes and Goodley 1961) although the general pattern is of a seaward-flowing freshwater layer which mixes with inflowing water from the North Channel. Edwards *et al.* (1986) estimate a residence time in the Outer Firth of approximately two months for water at depths ≤ 50m. Processes of deep-water renewal across the Great Plateau and Davaar Sill have also been described by Edwards *et al.* (1986). Between autumn and winter, pulsed inflows of denser, North Channel water occur across the Great Plateau into the Arran Deep and

over the Davaar Sill into Kilbrannan Sound; during spring the shallower depth of the Davaar Sill restricts inflow via this route. Water entering the Arran Deep via the Great Plateau flows northwards at a speed of about 1 to 2cms^{-1} and is uplifted at a rate of about 1mday^{-1}. Transit time for this water through the Arran Deep is estimated to be about one month. During summer the deep water mass throughout the fjord is typically isolated beneath a thermocline and halocline.

2.3 OBSERVATIONS RELEVANT TO THE PRESENT STUDY

2.3.1 Temperature and Salinity

2.3.1.1 March 1987

Contoured plots of temperature and salinity for the study area in March 1987 at 10m and 30m are shown in Figures 2.4 and 2.5, respectively. (Information regarding station numbers referred to througout this section can be found in Appendices 1 and 2 while station positions are shown in Figure 3.1). The salient feature of the plots, both at 10m and 30m is the presence of the Islay Front midway along the Malin Shelf. The front was manifest primarily as a temperature gradient, although there was a corresponding, but weaker, salinity gradient. Temperatures at both depths showed a progressive increase with distance offshore (Figures 2.4a and 2.5a). Salinities exhibited a similar trend (Figures 2.4b and 2.5b) and the Great Plateau Front located at the entrance to the Firth of Clyde was clearly visible at both 10 and 30m. This front was not evident in the corresponding temperature plots.

In addition to the contoured plots, depth profiles of temperature and salinity are shown in Figures 2.6 and 2.7 for a station representative of each of the four major areas of investigation. These profiles provide an indication of the degree of stratification in the

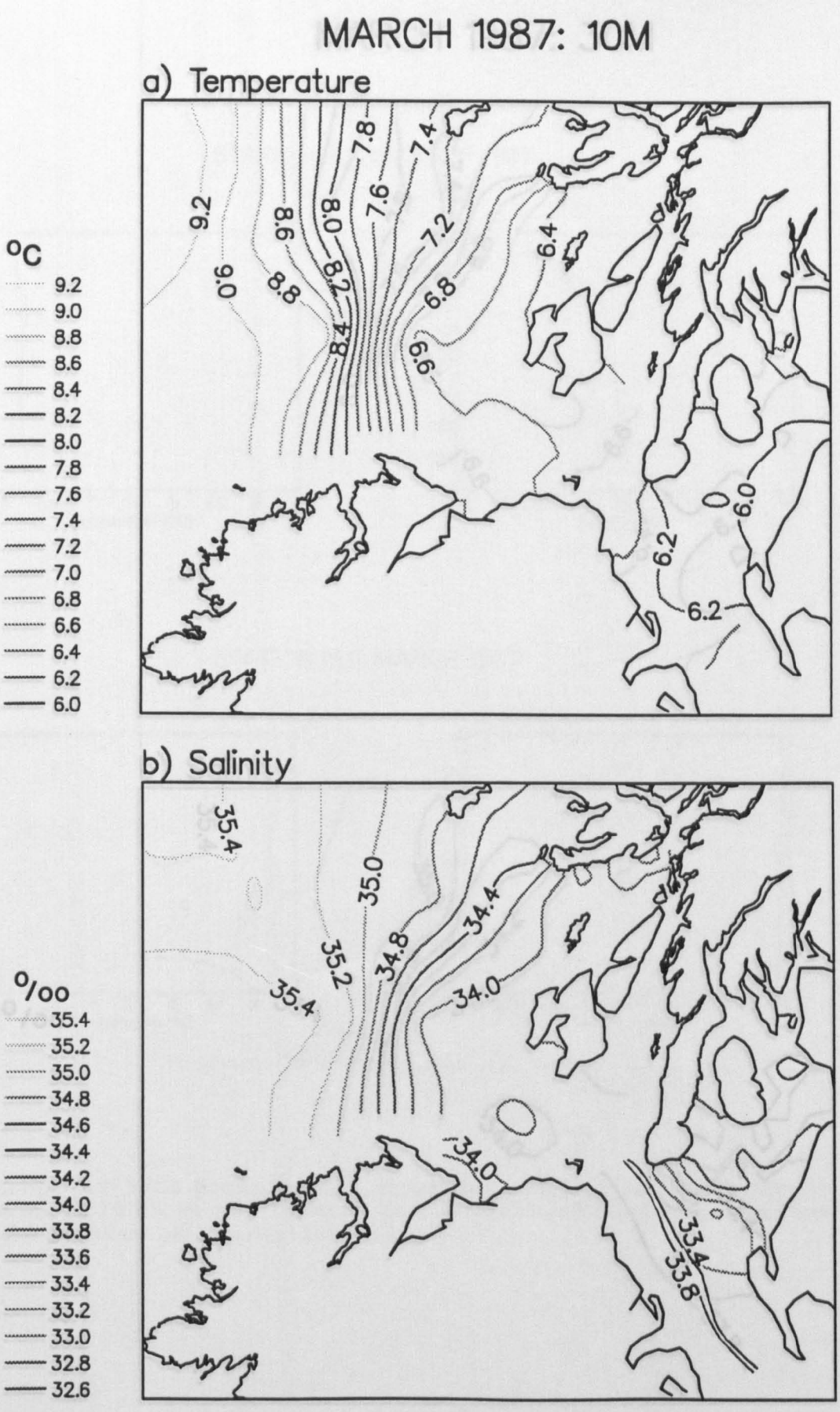


Figure 2.4 Temperature (a) and salinity (b) contours for the area of investigation in March 1987 at 10m depth.

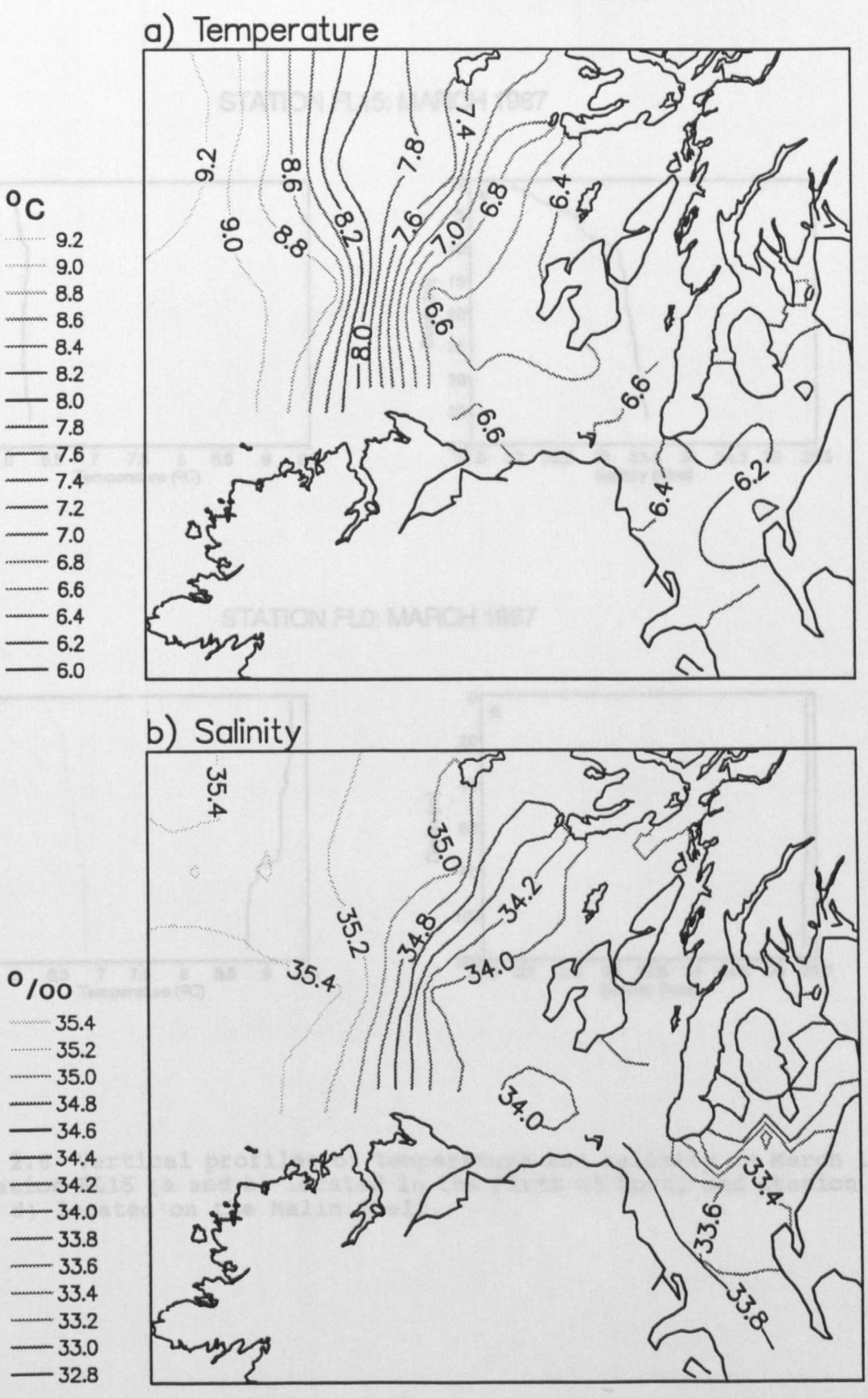


Figure 2.5 Temperature (a) and salinity (b) contours for the area of investigation in March 1987 at 30m depth.

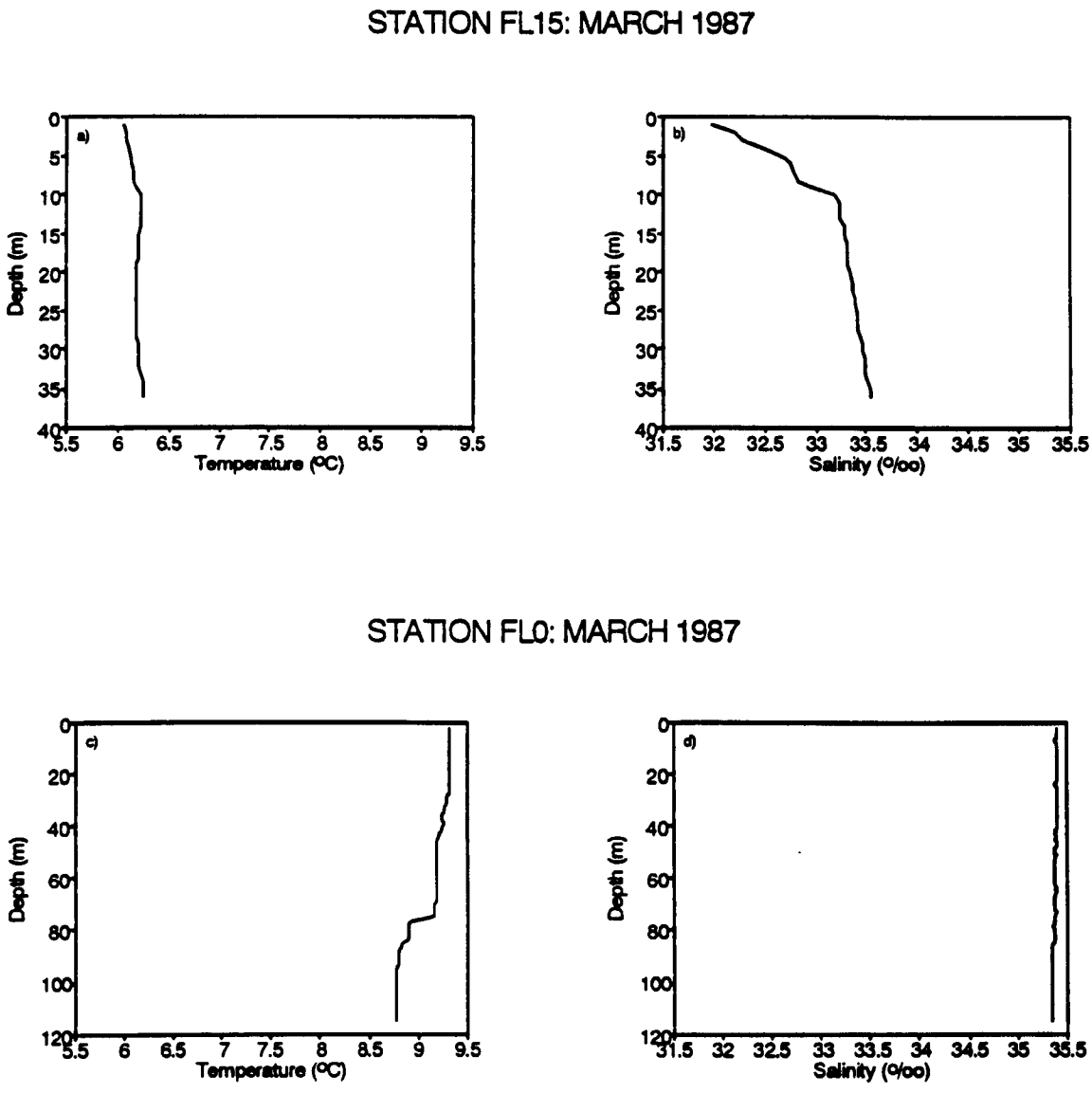


Figure 2.6 Vertical profiles of temperature and salinity in March 1987 for station FL15 (a and b) located in the Firth of Lorn, and station FL0 (c and d) located on the Malin Shelf.

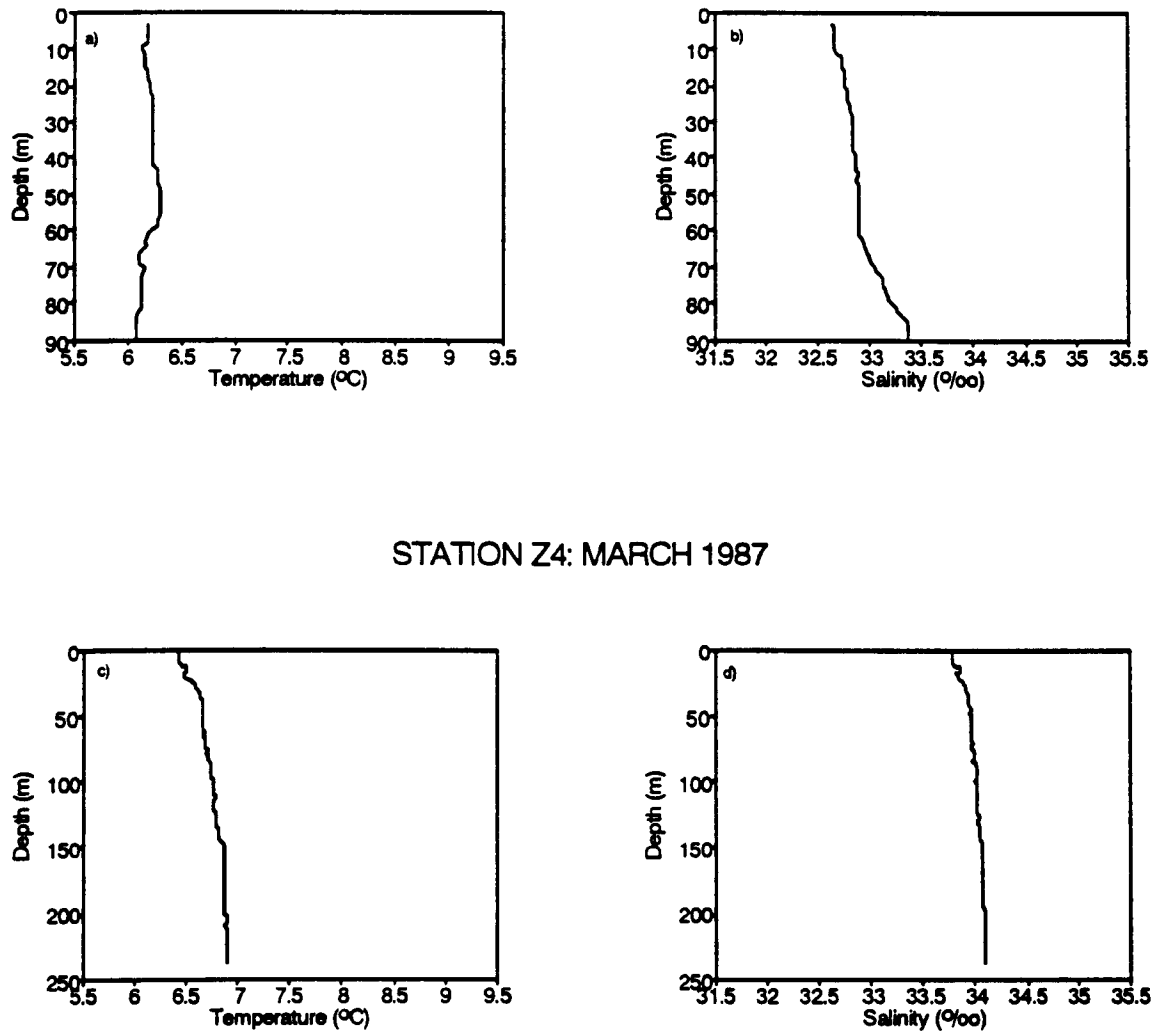


Figure 2.7 Vertical profiles of temperature and salinity in March 1987 for station AB30 (a and b) located in the Firth of Clyde, and station Z4 (c and d) located in the North Channel.

water column at the time of sampling.

In the Firth of Lorn, represented by station FL15, the water column was isothermal near 6°C (Figure 2.6a). A well-developed halocline was present in the upper 10m, below which salinities showed a gradual increase to about 33.5°/oo (Figure 2.6b).

On the Malin Shelf the upper 75m of the water column was well-mixed with respect to both temperature and salinity (Figure 2.6c and d). This water-mass was relatively warm and saline at near 9.3°C and 35.4°C. Below 75m temperatures gradually decreased while salinities remained nearly constant.

In Figure 2.7a and b, depth profiles of temperature and salinity are shown for station AB30 located in the Firth of Clyde. It should be noted that due to its vast size and varying topography, stations within the Firth of Clyde will exhibit considerably greater local variability in water properties than is likely to be encountered in the remaining study locations. Therefore, station AB30 should be regarded as representative only of the 'deep-water' stations within the firth. At station AB30 there were no clear signs of either temperature or salinity stratification (Figure 2.7a and b). Temperatures were near 6°C throughout the water column while salinities varied between about 32.7 to 33.4°/oo and increased with depth.

In the North Channel, represented by station Z4, the water column was also well-mixed with no signs of stratification in the TS profiles (Figure 2.7c and d). Both temperatures and salinities increased gradually with depth but the range of values was minimal: 6.5 to 6.9°C for temperature and 33.8 to 34.1°/oo for salinity.

2.3.1.2 May 1986

Contoured plots of temperature and salinity are shown for the area of investigation in May 1986 at 10m and 30m depth in Figures 2.8 and

2.9, respectively. The salient feature of the plots remains the Islay Front which was more defined, and slightly inshore, than observed during the March cruise. The front remained manifest primarily as a temperature gradient altough a corresponding, weaker, salinity gradient was evident. Temperatures and salinities increased with distance offshore, similar to the trend observed in March, and warmer, though less saline, water was present on the Malin Shelf in May.

In the Firth of Clyde the Great Plateau Front located at the firth entrance was evident in the salinity profiles (Figures 2.8b and 2.9b) though not in the corresponding temperature profiles (Figures 2.8a and 2.9a). Salinities in the firth were greater than in March and the 34°/$_{oo}$ isohaline, used to delineate the Scottish Coastal Current, was evident along the North Channel and extended to the edge of the Great Plateau Front.

Depth profiles of temperature and salinity at a station representative of the four main regions are shown for the May cruise in Figures 2.10 to 2.11.

At station FL15, located in the inner Firth of Lorn, the water column was nearly isothermal (Figure 2.10a) during the May cruise. Overall, temperatures ranged from between approximately 7 to 7.5°C and decreased with depth. The corresponding salinity profile exhibited a halocline between 5 and 10m below which salinity increased steadily with depth (Figure 2.10b).

The temperature profile for station FL1 on the Malin Shelf showed a warm (9.5°C), isothermal surface layer in the upper 20m of the water column (Figure 2.10c). Below this, at depths of 20 to 100m temperatures gradually decreased to <8.5°, followed by an isothermal bottom layer. The salinity profile indicated an isohaline water column, near 35.4°/$_{oo}$ (Figure 2.10d).

In the Firth of Clyde the temperature profile at station AB30 clearly indicated a well-developed thermocline in the upper 5m (Figure

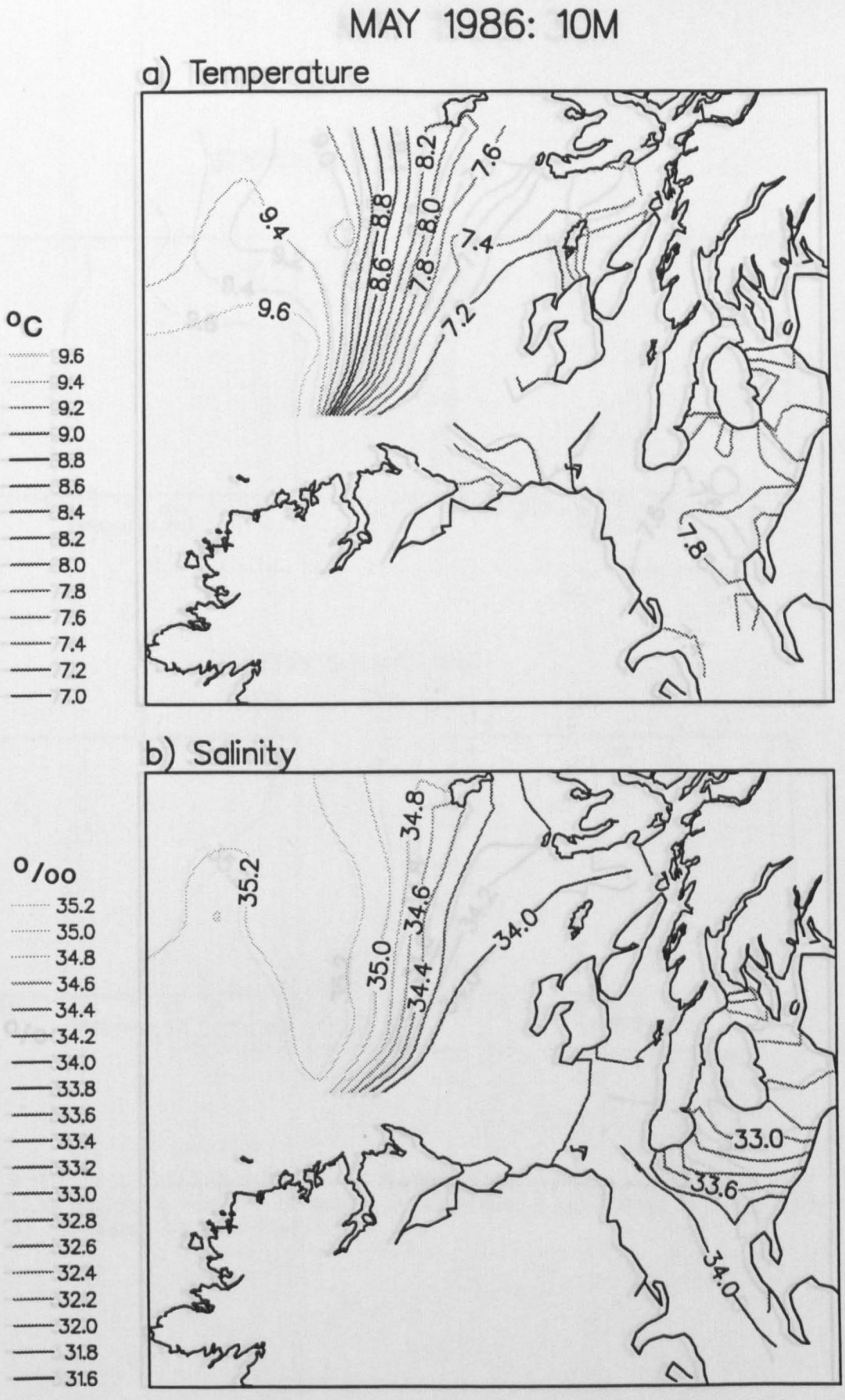


Figure 2.8 Temperature (a) and salinity (b) contours for the area of investigation in May 1986 at 10m depth.

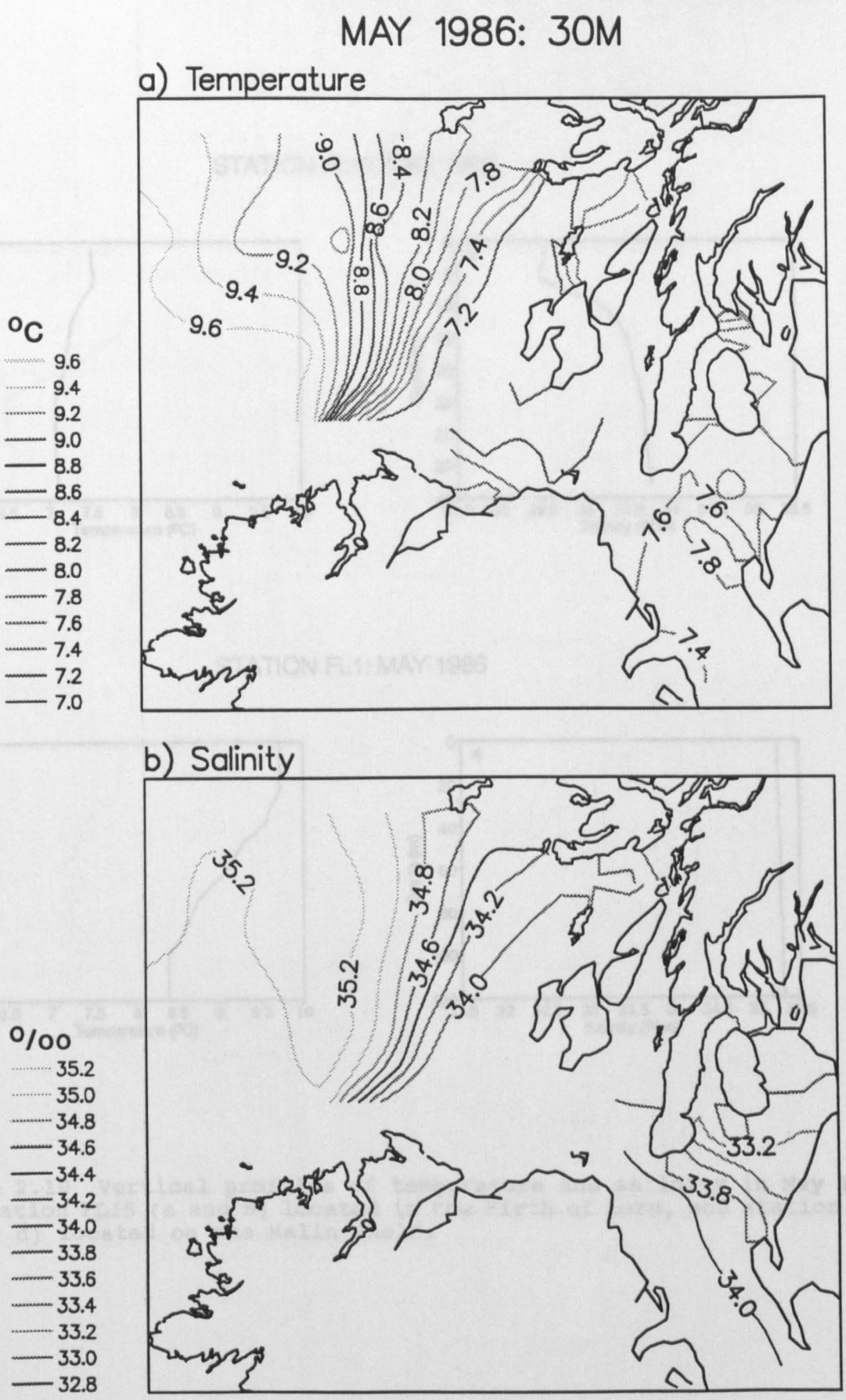
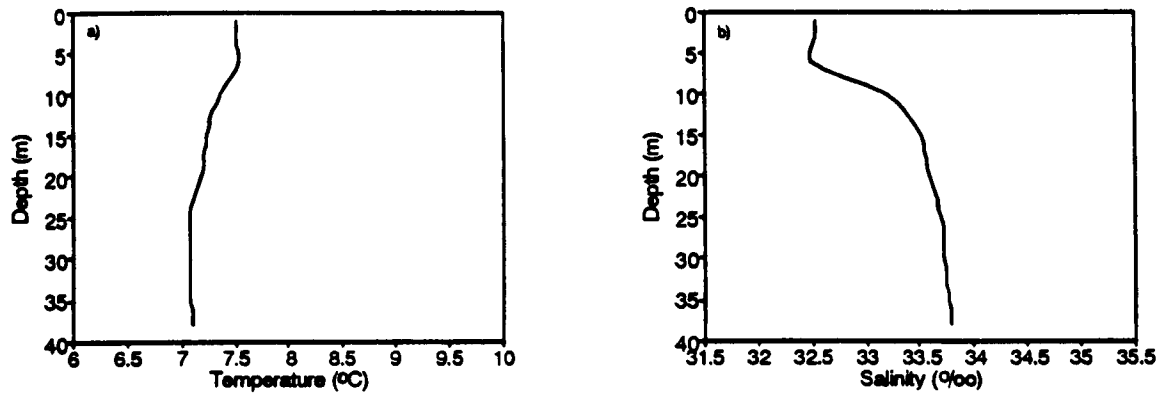


Figure 2.9 Temperature (a) and salinity (b) contours for the area of investigation in May 1986 at 30m depth.

STATION FL15: MAY 1986



STATION FL1: MAY 1986

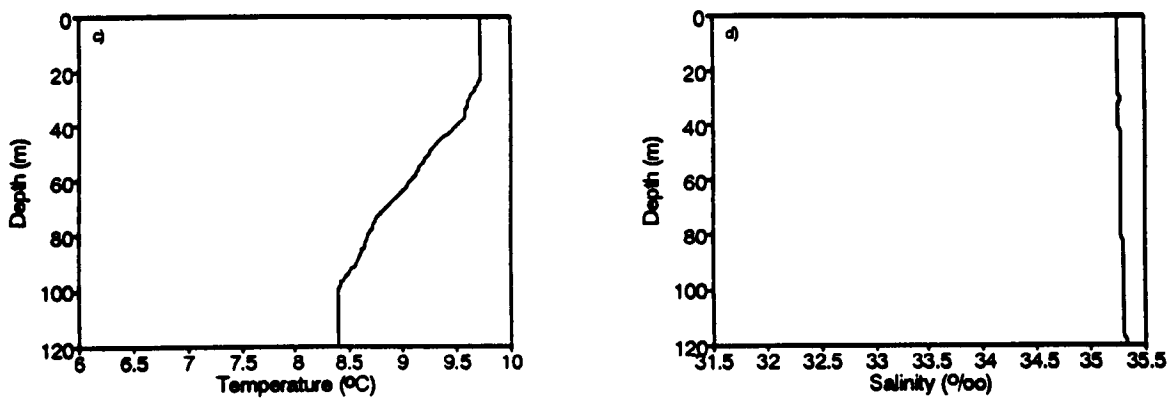


Figure 2.10 Vertical profiles of temperature and salinity in May 1986 for station FL15 (a and b) located in the Firth of Lorn, and station FL1 (c and d) located on the Malin Shelf.

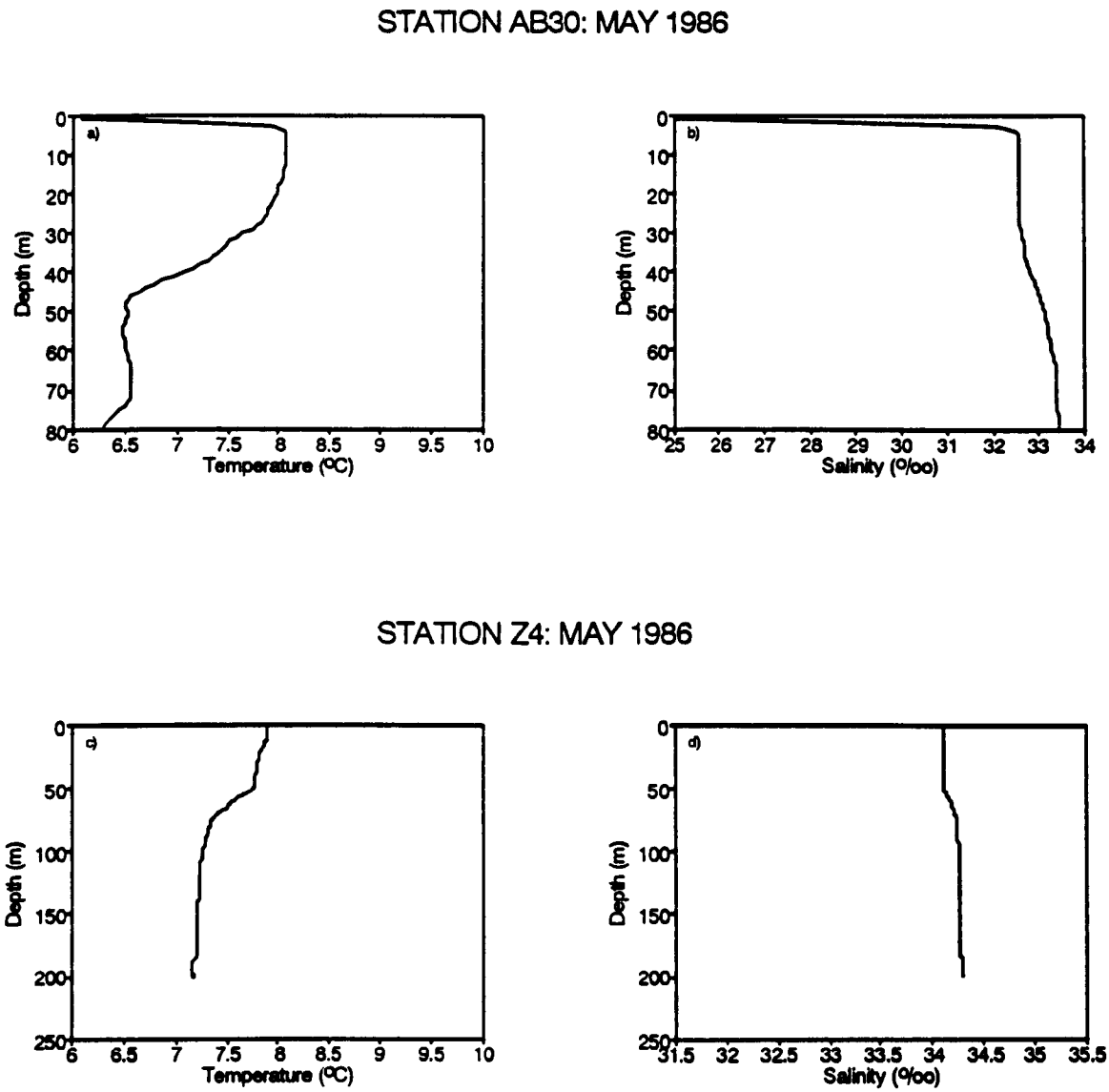


Figure 2.11 Vertical profiles of temperature and salinity in May 1986 for station AB30 (a and b) located in the Firth of Clyde, and station Z4 (c and d) located in the North Channel.

2.11a). Between 5 and 50m was a tongue of warm water below which temperatures gradually decreased to about 6.3°C. The cooler near-surface layer corresponded with a halocline (Figure 2.11b), and salinities between approximately 32 and 33°/₀₀. Below the halocline salinities gradually increased to near 34.5°/₀₀.

In the North Channel, the water column exhibited weak stratification between 55 and 75m with respect to both temperature and salinity (Figure 2.11c and d). The upper 50m of the water column was characterised by slightly warmer and fresher water (T ~ 7.8°C and S ~ 34.2°/₀₀) below which temperatures gradually decreased to near 7.2°C and salinities increased to about 34.4°/₀₀.

2.3.2 Phytoplankton Biomass and Primary Production

2.3.2.1 March 1987

Phytoplankton biomass, expressed as mean chlorophyll *a* values for the upper 30m of the water column, are shown for stations sampled in March 1987 in Table 2.1. At the time of the cruise biomass was highest in the inner regions of the Firth of Lorn (stations FL15 and FL13), generally low on the Malin Shelf (e.g. station FL1) and variable, though not attaining the levels observed in the Firth of Lorn, throughout the Firth of Clyde and the North Channel (Table 2.1).

Total column production in the Firth of Clyde, Firth of Lorn and on the Malin Shelf was estimated using photosynthetic parameters obtained from populations examined at representative stations. At the time of the March cruise production rates were 48mg C m^{-2} day^{-1} in the Firth of Clyde, 25mg C m^{-2} day^{-1} in the Firth of Lorn, and 84mg C m^{-2} day^{-1} on the Malin Shelf (Matthews 1987).

Measurements of size-fractionated chlorophyll *a* biomass and primary production were also made at a station representative of each

Table 2.1 Mean values of chlorophyll *a* (mg m^{-3}) for the upper 30m of the water column at stations sampled in March 1987. Dip No. is the corresponding CTD dip number for the station. Station positions are shown in Figure 3.1.

Station	Dip No.	Chlorophyll *a*
FL15	111	1.29
FL13	109	0.62
FL12	103	0.09
FL9	100	0.15
FL1*	92	0.11
D0	90	0.15
D4	86	0.18
D7	83	0.15
C5	80	0.18
C3	78	0.14
A4	74	0.10
A2	72	0.17
Y3	65	0.17
Y1	58	0.29
AB1	56	0.23
AB3A	57	0.23
AB5	52	0.14
AB8	49	0.12
AB14	43	0.20
AB15	68	0.13
AB17	70	0.15
AB20	40	0.16
AB22	38	0.14
AB25	33	0.16
AB28	30	0.22
AB30	28	0.14
AB34	16	0.17
AB35A	18	0.19
AB38	9	0.17
AB38A	10	0.21
AB40	12	0.12
AB44	6	0.22
Z4	61	0.13

* used for station FL0 (dip 91) as chlorophyll data were unavailable for this station

area (Table 2.2). In both the Firth of Clyde (station AB30) and Firth of Lorn (station FL12) phytoplankton biomass and primary production were highest in the >5μm size fraction. On the Malin Shelf (station FL0) the greatest proportion of phytoplankton biomass and production occurred in the 1 to 5μm size class, although the production rate remained comparable

Table 2.2 Chlorophyll *a* biomass (Chla), phaeopigments (Phaeo), acid ratio (A.R.) and percent of total chlorophyll *a* (%Total Chla) and primary production (%Total Prod) in size fractionated phytoplankton samples collected at three stations during the March cruise. Station AB30 is located in the Firth of Clyde, FL12 in the Firth of Lorn, and FL0 on the Malin Shelf. Chlorophyll *a* and phaeopigment units are mgm^{-3}. All samples are from 10m. Productivity incubations were conducted at irradiance levels of ca. 700μE m^{-2} s^{-1}. Station positions are shown in Figure 3.1.

Fraction	Station	Chla	Phaeo	A.R.	%Total Chla	%Total Prod
	AB30	0.59	1.04	1.41	74	75
>5μm	FL12	0.38	0.12	1.85	59	62
	FL0	0.10	0.08	1.64	32	42
	AB30	0.19	0.24	1.50	24	12
<5μm->1μm	FL12	0.18	0.09	1.78	28	32
	FL0	0.18	0.13	1.65	58	44
	AB30	0.02	0.06	1.31	2	13
<1μm	FL12	0.08	0.01	2.04	12	5
	FL0	0.03	0.03	1.48	10	14

to that in the >5μm size class. The <1μm size fraction did not account for a substantial proportion of either phytoplankton biomass or productivity in any of the areas sampled.

2.3.2.2 May 1986

Mean values of chlorophyll *a* biomass for the upper 30m of the water column at stations sampled in May 1986 are given in Table 2.3. During this cruise, the highest phytoplankton biomass occurred in Loch Fyne (station AB44) near the head of the Firth of Clyde. Throughout the firth biomass was generally increased over levels observed in the North Channel, although comparable values were recorded at station C1. Along the Firth of Lorn - Malin Shelf transect, biomass was high at stations on either end (i.e FL15 and FL1, respectively) and lower at intermediate locations.

Estimates of total column production were also made during the May

Table 2.3 Mean values of chlorophyll *a* (mg m^{-3}) for the upper 30m of the water column at stations sampled in May 1986. Dip No. is the corresponding CTD dip number for the station. Station positions are shown in Figure 3.1.

Station	Dip No.	Chlorophyll *a*
FL15	3	0.46
FL12	6	0.09
FL12	12	0.10
E2	15	0.15
FL8	24	0.10
M3	29	0.26
FL1	33	0.45
C6	119	0.18
C3	116	0.23
C1	81	0.49
A3	46	0.18
Y5	48	0.23
Y3	52	0.51
AB3A	54	0.47
AB5	109	0.14
AB8	62	0.55
AB17	103	0.34
AB30	93	0.50
AB38	84	0.46
AB40	81	0.49
AB44	98	0.76
Z4	111	0.22

cruise. At this time productivity was greatest within the Firth of Clyde at 584mg C m^{-2} d^{-1}, somewhat lower on the Malin Shelf at 365mg C m^{-2} d^{-1}, and only 71mg C m^{-2} d^{-1} in the Firth of Lorn (SMBA Annual Report 1987).

Size fractionation of phytoplankton samples provided additional information regarding the distribution of algal biomass and rates of primary production within the size classes examined (Table 2.4). Within the Firth of Clyde, phytoplankton in the >5μm size fraction contributed the most to total production although the greatest proportion of plant biomass occurred in the 1 to 5μm fraction; the latter size fraction also made a considerable contribution to the overall production. This was not the case in the Firth of Lorn where both maximum productivity and biomass levels were found in the >5μm size fraction. On the Malin Shelf, the greatest production rates were measured in the >5μm size class

although the corresponding biomass level was low. Similarly, the high algal biomass observed in the 1 to 5μm size fraction accounted for only a small proportion of the total productivity. In all areas the relative proportion of biomass and total production accounted for by the <1μm size fraction was low, although there was some variability (Table 2.4).

Table 2.4 Chlorophyll *a* biomass (Chla), phaeopigments (Phaeo), and percent of total chlorophyll *a* (%Total Chla) and primary production (%Total Prod) in size fractionated phytoplankton samples collected at three stations during the May cruise. Station AB30 is located in the Firth of Clyde, FL12 in the Firth of Lorn, and FL1 on the Malin Shelf. Chlorophyll *a* and phaeopigment units are mgm^{-3}. All samples are from 10m. Productivity incubations were conducted at irradiance levels of ca. 200μE m^{-2} s^{-1}. Station positions are shown in Figure 3.1.

Fraction	Station	Chla	Phaeo	A.R.	%Total Chla	%Total Prod
	AB30	0.59	0.04	1.96	17	54
>5μm	FL12	0.37	0.11	1.78	63	76
	FL1	0.77	0.10	1.90	50	66
<5μm->1μm	AB30	2.61	0.01	2.02	77	40
	FL12	0.19	0.07	1.75	32	17
	FL1	0.31	0.08	1.82	20	21
<1μm	AB30	0.19	0.13	1.61	6	6
	FL12	0.03	0.04	1.49	5	7
	FL1	0.46	0.08	1.86	30	13

3. METHODS

3.1 SAMPLING PROGRAMME

Zooplankton were examined from samples collected during two cruises to the study area. The first cruise took place from 14 to 25 May 1986 aboard the R.V. G.A. Reay and the second took place from 19 to 27 March 1987 aboard the R R S Frederick Russell. On each cruise, zooplankton were collected at stations routinely sampled as part of the Lorn/Clyde project initiated at Dunstaffnage Marine Laboratory in May 1986. Sampling details for all stations visited are given for the May 1986 cruise in Appendix 1 and the March 1987 cruise in Appendix 2. Station locations are shown in Figure 3.1.

At each station, zooplankton samples were collected at 10m and 30m, depth permitting, using a Flygt submersible pump (model CS3085), capable of delivering $1m^3min^{-1}$. For sampling, the pump was lowered by crane to approximately 1 to 2m below the sea surface. Water was pumped from the required depth, using a heavy-duty rubberized intake hose 7.6cm (i.e. 3in) in diameter, through a connecting hose of the same material, into a collecting tank onboard ship (Figure 3.2). The water then passed through a parallel series of three filters which separated the sample into a coarse (>1000μm), medium (1000μm-330μm), and fine (330μm-180μm) size fraction, although at some stations the coarse/medium or medium/fine size fractions were combined. The volume of water filtered was measured independently for each size fraction by a flowmeter mounted at the base of the filter tube. In general, samples were collected over the time period required for ~$1m^3$ of water to pass through the fine filter; ~5 mins. A photograph of the plankton pump onboard the R R S Frederick Russell is shown in Figure 3.2.

Following collection, most samples were split into two halves

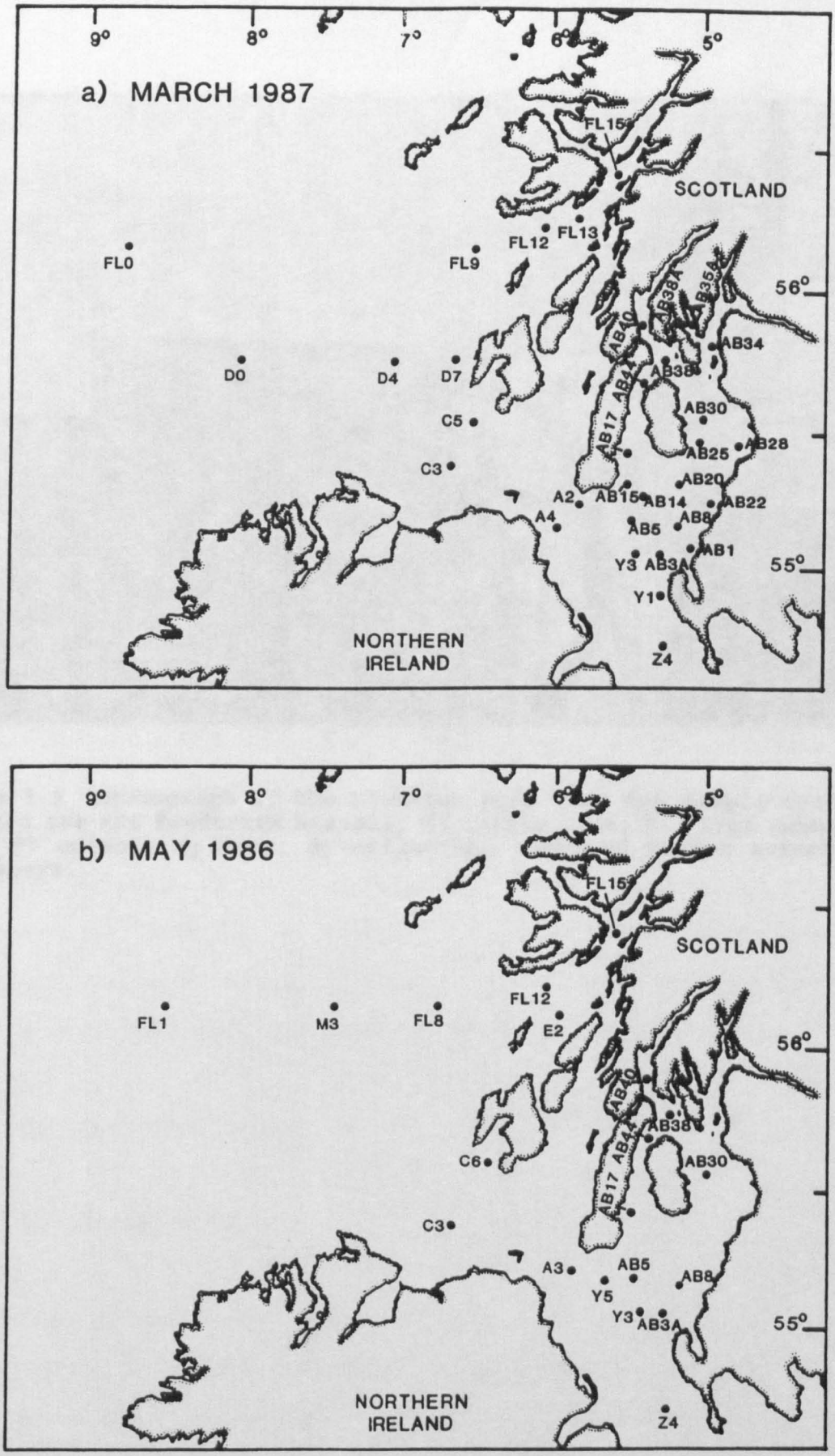


Figure 3.1 Station locations for March 1987 (a) and May 1986 (b).

Figure 3.2 Photograph of the plankton pump used for sample collection on board the RRS Frederick Russell. a) intake hose, b) Flygt submersible pump, c) connecting hose, d) collecting tank, e) filter assembly, f) flowmeters.

using a Motoda plankton splitter. One half of the sample was preserved for taxonomic study in 5% formaldehyde while the second half was frozen for use in a separate study. The coarse fraction was generally not split due to the small amount of material collected.

During both the May 1986 and March 1987 cruises, vertical profiles of conductivity, temperature and depth were made using a Plessey CTD at the majority of stations visited. Water samples were also routinely collected from discrete depths for the measurement of chlorophyll *a*. Profiles of chlorophyll *a* were constructed for each station at which zooplankton were collected by plotting the discrete values against depth. An integrated value of chlorophyll *a* was then obtained for the upper 30m of the water column, roughly corresponding to the euphotic zone, using the Kontron IPSx image analysis system. This value was divided by the total integrated depth (usually 30m but occasionally less) to obtain a depth independent measure of phytoplankton biomass expressed as mg m^{-3}.

More detailed information regarding the collection of both CTD and chlorophyll *a* data can be found in the R.V. G.A. Reay and R.R.S. Frederick Russell cruise reports (Matthews 1986*a*, 1987) and corresponding SMBA Internal Reports (Jones 1988*a* and *b*).

3.2 LABORATORY PROCESSING

3.2.1 Displacement Volume

Standing stock was estimated for each sample as displacement volume, using a 'plankton chamber' constructed out of perspex (Figure 3.3). To measure displacement volume the sample was placed in the cylindrical tube, which had a 180μm mesh at the base, and carefully blotted to remove all excess water. The chamber was then sealed and filled with filtered seawater (Whatman GF/C filters) from a 10.00 ±

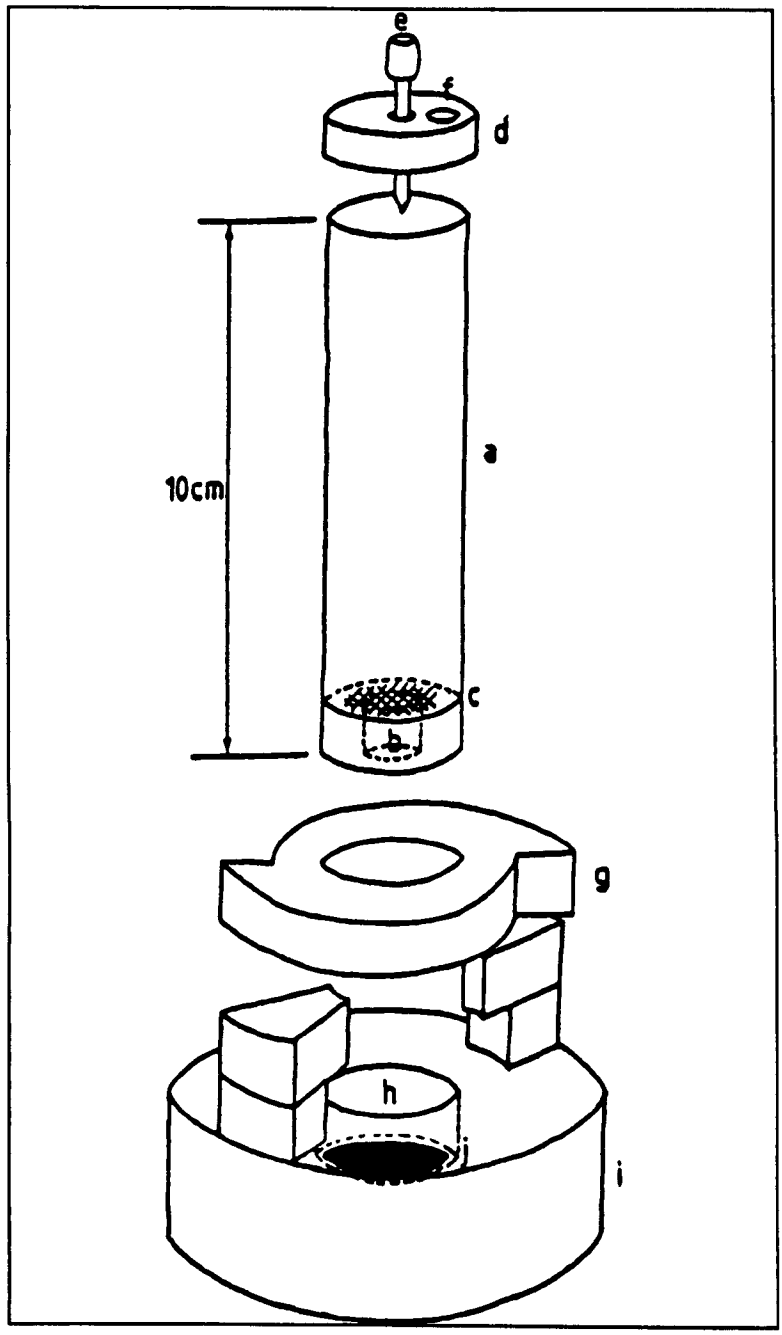


Figure 3.3 Diagram of the 'plankton chamber' used to measure sample displacement volume. The chamber a) contains the sample. Excess water from the sample is drained through the hole b) covered by 180μm gauze c). The top d) has two holes; through the central hole is placed a metal pin e), and through the second hole f) is placed the tip of a 25ml burette. The plankton chamber is secured by the locking device g) in the shallow well h) of the perspex base i). The bottom of the well contains a rubber seal j) to provide a water-tight fit. From Wren (1991).

.01ml burette until the water surface was broken by the tip of the metal pin. This volume was subtracted from the volume of the chamber when empty to obtain the zooplankton displacement volume. The empty chamber volume was calculated as the mean value of three readings and was recalibrated after every tenth sample to check for compression in the rubber disk which sealed the chamber.

In general, subsamples were measured in their entirety. However, on occasion large gelatinous zooplankters and/or larval fish present in the samples were removed prior to determining the displacement volume. All biomass measurements were recorded as ml m^{-3}. The expression of biomass as a volume rather than a weight measurement is routine in the study of zooplankton (e.g Beers 1976; Omori and Ikeda 1984). An approximate conversion of displacement volume to dry weight and ash-free dry weight can be made using the following equation from Matthews and Heimdal (1980): 1ml displacement volume = 1g wet weight = 0.2g dry weight = 0.1g C.

3.2.2 Subsampling Procedure

Subsampling was used to obtain estimates of zooplankton abundance for those samples containing greater than approximately 200 animals. With the exception of two samples in the first cruise which were subsampled using a Stempel pipette, all subsampling was conducted using a compartmental plankton splitter which divided the sample into two halves. Samples were split until an aliquot containing between approximately 50 to 75 animals was obtained and at least three aliquots were counted for a minimum of 200 animals. When necessary, a fourth aliquot was counted to obtain the minimum number of individuals required.

There are many factors which affect the performance of subsampling devices and how accurately they reflect the true abundance of animals

in the wild. The error due to subsampling is generally thought to be minimal compared to that associated with the sample collection (e.g. Minello and Matthews 1981; de Nie and Vijverberg 1985), although this is not always the case (Van Guelpen *et al.* 1982). Factors such as entanglement (Horwood and Driver 1976) and over-dilution (Lewis and Garriot 1971; Longhurst and Seibert 1967) tend to decrease the accuracy of the population estimates. These are offset by increasing the number of animals counted per subsample (Van Guelpen *et al.* 1982) or by counting replicate subsamples (Horwood and Driver 1976) both of which are known to reduce sampling error.

There are also statistical problems which accrue through the use of repeated sampling divisions. This is because the error associated with the repeated halving of a sample is not independent but increases with the number of successive splits (Van Guelpen *et al.* 1982). It is not clear, however, whether sampling error is reduced by using a multiple-compartment splitting device (Van Guelpen *et al.* 1982; Horwood and Driver 1976).

Several studies have focused on the statistical error associated with subsampling zooplankton using standard devices such as the Folsom and Motoda plankton splitters, and the stempel pipette (e.g. Van Guelpen *et al.* 1982; Horwood and Driver 1976; Frolander 1968). Van Guelpen *et al.* (1982) in their comparison of subsampling devices found that the level of precision ranged from 5 to 31% (expressed as a coefficient of variation). Alden *et al.* (1982) provided a set of equations which enable the level of subsampling error to be pre-determined and kept constant for all taxa examined. They maintained that an error of <30% was reasonable for most zooplankton sampling programmes, which would require counting approximately 45 individuals per species, per subsample. Tett (1987) recommended selecting a subsample which contained approximately 100 individuals of the most abundant species to obtain a subsampling error near ± 10%.

In the present study 60% of all samples were examined whole or after splitting into two halves at the time of collection. Of the remaining samples, 95% were examined after ≤6 splits (i.e. 1/64 of the entire sample). Only 11 samples were split into smaller fractions. The median number of animals counted for the dominant taxa was 95.5 individuals per subsample, with an overall range of 43 to 300 individuals.

During the processing of samples, the subsampling device was tested for bias by placing 100ml of water in the chamber and measuring the volume in each compartment following a typical split. Ten replicates were conducted and on all occasions but one, the proportion of the sample in each compartment was equal at 50ml. On the other occasion the split varied by ± 0.5mls (i.e. 49.5ml and 50.5ml). Therefore, subsamples were always chosen at random with respect to the chamber compartment and it was assumed that no additional error was introduced by doing so.

The performance of the plankton splitter was also evaluated on six occasions by comparing population estimates obtained from the subsamples with that for the whole sample. In each case individuals from three replicate subsamples representing 1/4 of the sample were enumerated. The results of a representative trial are shown in Table 3.1. Results from the remaining trials can be found in Appendices 3 to 7. On all occasions, the population estimates obtained for individual taxa from the subsamples showed good agreement with the overall number, although the subsampling precision, measured as the coefficient of variation, was generally much higher than that reported by Van Guelpen *et al.* (1982).

The wide geographical range covered in the study combined with the temporal scale and the large number of taxa examined, made it impracticable to apply the methodology outlined by Alden *et al.* (1982) which maintains a uniform level of subsampling error. However, given the numbers enumerated for the most abundant taxon in each subsample, and the good agreement between the population estimates and total numbers

Table 3.1 Results from the first zooplankton sample examined to evaluate the performance of the subsampling device. Each subsample (SS1 to SS3) represents 1/4 of the total sample. $\tilde{N}$ is the population estimate based on the three subsamples. N is the total number for the whole sample. $\bar{x}$ is the mean value per three subsamples. s is the standard deviation. CV is the coefficient of variation ($100 \cdot (s/\bar{x})$); - indicates value could not be calculated. Taxa are arranged according to increasing coefficients of variation.

Species	SS1	SS2	SS3	$\bar{x}$	$\tilde{N}$	N	s	CV
Copepod nauplii	10	13	8	10.33	41.33	39	2.52	24
Acartia clausi	4	6	4	4.67	18.67	18	1.15	25
Cirripede nauplii	8	8	13	9.67	38.67	38	2.89	30
Microcalanus spp.	5	6	3	4.67	18.67	16	1.53	33
Euphausiid nauplii	7	3	5	5.00	20.00	21	2.00	40
Oithona spp.	7	4	3	4.67	18.67	20	2.08	45
Calanus spp.	5	3	8	5.33	21.33	25	2.52	47
Thysanoessa raschii	2	3	1	2.00	8.00	7	1.00	50
Electra pilosa	4	1	3	2.67	10.67	9	1.53	57
Temora longicornis	2	0	2	1.33	5.33	7	1.15	87
Unidentified copepodids	0	2	2	1.33	5.33	5	1.15	87
Polychaete larvae	2	1	0	1.00	4.00	4	1.00	100
Appendicularians	0	1	0	0.33	1.33	1	0.58	173
Unidentified eggs	0	4	0	1.33	5.33	4	2.31	173
Evadne nordmanni	1	0	0	0.33	1.33	1	0.58	173
Bivalve larvae	0	2	0	0.67	2.67	4	1.15	173
Centropages hamatus	0	0	1	0.33	1.33	1	0.58	173
Oithona similis	0	0	0	0.00	0.00	1	0.00	-

obtained during the evaluation trials, it is reasonable to assume that the estimates of zooplankton abundance obtained in the present study are adequate for the examination of large-scale processes.

3.2.3 Taxonomic Identification

All zooplankton were identified using a Wild-M5 dissecting microscope. The taxonomic level to which an individual was classified varied among the different 'groups' of zooplankton examined. As the main focus of the study was the copepod fauna, copepods were identified to species as much as possible, although individuals belonging to *Pseudocalanus*, *Microcalanus*, and *Oithona* were identified only to genus. In the case of *Pseudocalanus*, following the recent work of Frost (1989),

it is likely that the specimens examined in this study were of *Pseudocalanus elongatus* Boeck. Specimens of *Microcalanus* were believed to be a mixture of *Microcalanus pusillus* G.O. Sars and *M. pygmaeus* (G.O. Sars) while *Oithona similis* Claus was thought to be the predominant species of this genus although *O. plumifera* Baird, and possibly others, were also present.

Throughout the text, copepodid stages one to five are denoted by the abbreviations C1 to C5, and adults by C6. In the case of *Calanus*, only adults and C5's were identified to species due to the difficulty in distinguishing between the earlier copepodid stages of *Calanus finmarchicus* (Gunnerus) and *C. helgolandicus* (Claus) (see Marshall and Orr, 1955) which both occurred throughout the study area. However, based on the distribution and relative abundance data obtained for the two species from the samples collected (see section 4.2.2) it would appear that most specimens were of *C. finmarchicus*. Early copepodid stages (i.e. C1 to C3) of several species were grouped together as 'unidentified copepodids'. This group contained primarily individuals of *Paracalanus parvus* (Claus), *Centropages hamatus* (Lilljeborg), *Pseudocalanus* spp., and *Microcalanus* spp.

The number of C6 females and males was determined for all copepods with the exception of *Oithona* for which only the number of C6 males was recorded. Numbers of copepod nauplii were also recorded although no attempt was made at identification. For the March cruise, all *Calanus* copepodids examined were classified according to developmental stage.

Cladocerans, chaetognaths, amphipods, euphausiids, polychaetes (i.e. *Tomopteris*) and ectoproct larvae, known as cyphonautes, were also identified to species as much as possible. Meroplanktonic species were generally placed into larger taxonomic groupings: cirripedes were classified as either nauplii or cyprids; decapod larvae were identified to family; other larvae were classified only as 'bivalve', 'polychaete', 'gastropod' or 'echinoderm'. Numbers of appendicularians and gelatinous

zooplankton were also recorded although they were not identified due to their generally poor condition. For damaged appendicularians, only the trunk portion was counted as an individual.

Other groups (e.g. isopods, ostracods, anenomes, pycnogonids) occurred infrequently in the samples. These small numbers of individuals were generally noted and enumerated but no attempt was made at further identification. For a complete list of the species and taxa identified in the study, refer to Table 4.6 (see p. 127).

Literature used in the identification of species included Sars (1903, 1918), Rose (1933) for copepods; Einarsson (1945), Mauchline (1971) for euphausiids; Fraser (1957) for chaetognaths; Williamson (1957) for decapod larvae; Dunbar (1963) for amphipods; Ryland (1965) for cyphonautes; Ramner (1939) for cladocera.

3.3 IMAGE ANALYSIS

All samples were processed using a Kontron IBAS 20000 image processing system (Kontron Bildanalyse GMBH). The basic components of the system consist of an image processing unit, host computer operating on CP/M 2.2 software, data monitor and keypad, colour monitor, and digitizer tablet and mouse (Figure 3.4). The system operates using 256 grey levels, ranging from black (0) to white (255), and a standard image frame size of 512 X 512 pixels (a pixel being the smallest spatially-digitised unit of an image). Specific details regarding both hardware and software of the image processing system can be found in the manual: IBAS 2000 Automatic Measuring Program Description (Kontron 1985).

3.3.1 Practical Set-up

The initial step of any image analysis program is the entering of an image into the system for subsequent processing. This aspect of the

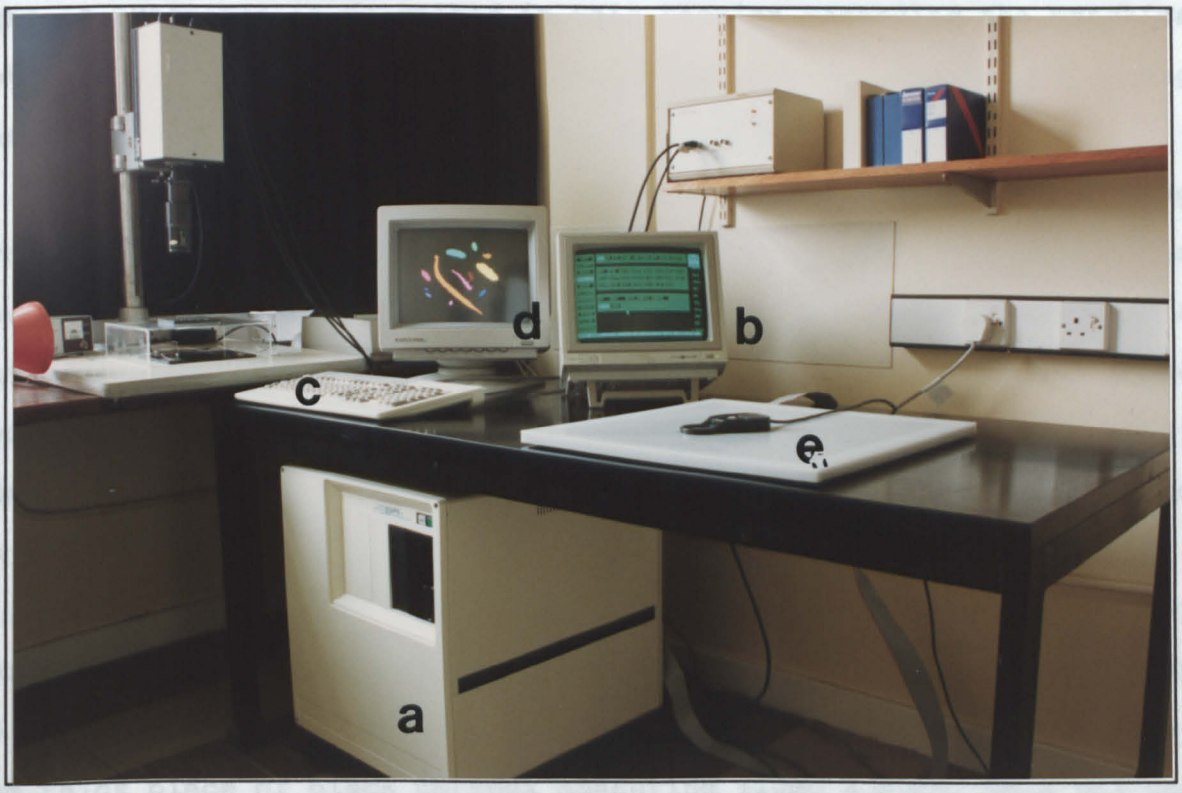


Figure 3.4 Photograph showing component parts of the image analysis system at Dunstaffnage Marine Laboratory. a) image processing unit and host computer, b) data monitor, c) keypad, d) colour monitor, e) digitizer tablet and mouse.

current programme is described in this section regarding the practical set-up used for the present study. The remaining components of the image analysis programme are discussed in section 3.3.2.

In the present study all images were entered into the image processing unit using a LINK Electronics video camera (Type 109B) which was calibrated to correct for distortion using an IBAS 2000 program. An external sync-pulse generator was used to provide synchronizing pulses for the video camera and monitor. The video camera was fitted with a 62mm macro-lens and magnification was kept near maximum (ca 15x) as much as possible.

To facilitate the processing of zooplankton, perspex sample trays were designed for use with the image analyser. To construct each tray, 20 holes of 10mm in diameter were drilled at regular intervals into a 5mm thick piece of black perspex measuring 110mm X 80mm. This was then attached using chloroform to a clear perspex base 3mm in thickness. A separate lid for each tray was also constructed out of clear perspex. Black perspex was used for the body of the tray as this minimized light reflection at the compartment edges; clear perspex was used for the base of the tray to enable light to shine through from below. Although the number of compartments in each tray (i.e. 20) was chosen arbitrarily, the compartment diameter of 10mm was chosen specifically to cover the approximate field of view of the video camera at 15X.

For processing, zooplankton were sorted into tray compartments containing either filtered seawater or 5% formaldehyde. Specimens were grouped according to species, and sex and developmental stage if known; this facilitated data collection as it was not possible to relate the individual measurements back to specific zooplankters. The sample tray was placed on a perspex table (22cm X 29cm) approximately 13cm in height, and positioned over an opening 9cm in diameter in the centre of the table. The light source for the sample tray was provided by four ultra-bright 0.2in light emitting diodes (L.E.D.s) connected to a Weir

Microreg Power Supply and operated at 5V. The L.E.D.s were arranged in a rectangular pattern and glued onto a piece of black perspex which was then positioned beneath the sample tray. This provided both lighting and a black background against which the zooplankton were viewed. By using a light source from beneath the sample tray, light reflection off both the compartment edges and the zooplankters themselves was minimized. Additional lighting, when necessary, was provided by a desk-lamp with a 60W bulb, positioned approximately 25cm away from the sample tray. The light from the desk-lamp was directed downwards and therefore still illuminated the zooplankton from below. A disadvantage to using the desk-lamp as a light source was that small particles of dirt, often present in the sample compartments, appeared more prominent then when illumination was by the L.E.D. source alone. The set-up used to process zooplankton samples examined in this study is shown in Figure 3.5.

3.3.2 Measuring Programme

A semi-automated measuring programme was used to process all zooplankton samples. No attempt was made to incorporate pattern recognition into the programme design. However, one consideration in designing the measuring programme was the fact that all images processed were to be permanently stored onto magnetic tape for future reference. The programme therefore attempted to maximize magnification while maintaining a field of view large enough to allow the processing of a reasonable number of individuals per image frame.

Once an image has been entered into the system, the remaining image analysis programme can be broken down into four basic components, which are as follows: 1) image enhancement 2) discrimination 3) measurement 4) data output. Details of these four components are outlined below.

Figure 3.5 Photograph showing set-up used to process zooplankton samples by image analysis. a) sample tray, b) perspex table, c) LED light source, d) desk lamp, e) video camera, f) printer.

1) Image enhancement:

Images were first corrected for uneven illumination using a shading-correction function. Since the zooplankton images were recorded against a black background, the shade reference image consisted of an image of a black background, entered using a multiple input function and then subjected to a median filter, both for noise reduction. Images were next enhanced to increase the contrast between the zooplankton and the background using a function which normalised the grey level values. Boundary edges, e.g. where the zooplankton and background grey levels merge, were also enhanced and delineated in order to correct for the "halo" problem. This arises in regions where objects of markedly different grey levels come into contact and a gradual change in grey level values at the interface may result in a "halo" effect thus enlarging the object size (Joyce-Loebl 1985).

2) Discrimination:

Discrimination is the step in image analysis where the objects of interest (in this case zooplankton) are distinguished from those not of interest (in this case the background). This is accomplished by setting an upper and a lower grey level boundary which encompasses the grey levels corresponding to the objects of interest, but not those of the background or other objects not of interest. Discrimination results in a binary image where all pixels within the boundaries selected are set to white while those outside are set to black.

In the present study all discrimination levels were set interactively, i.e. using the mouse and digitizing tablet, rather than automatically. Initial trials with the measuring programme, and the copepods in particular, showed considerable intra- and interspecific variation in grey levels thus making it impossible to select "overall" values for use in discrimination. Some of this variability appeared to be related to the organism size and for this reason, three size classes based on area (mm^2) were used for processing copepods from the samples.

The size fractions selected were: 'small': 0.01 to 0.18mm^2, 'medium': 0.15 to 0.75mm^2, and 'large' >0.5mm^2. Examples of taxa in each size fraction are *Oithona*, *Pseudocalanus*, and *Calanus*, respectively. Individuals within each size fraction were interactively discriminated to produce a binary image. Depending upon the size fraction, images were eroded (i.e. pixels were removed from objects according to the conditions specified) and then dilated (i.e. remaining objects were enlarged back to their original size) in order to exclude the antennae, appendages and urosome. Eroding also removed debris from the image background. A contouring function was then used to overlay the outline of the binary image back onto the original image to ensure that the two images corresponded closely (Figure 3.6).

Other taxonomic groups were not segregated according to size. Discrimination levels were set interactively and only a minimal amount of eroding and dilating was used prior to measurement. The contouring function was again used to check that the discriminated image provided a reasonable representation of the original.

3) Measurement:

The parameters selected for measurement were COUNT, MOMENT, and AREA, which enumerated, provided individual length and width, and area measurements, respectively. For copepods, the length and area measurements were for the cephalothorax. Given the range of species being measured, these measurements were regarded as being preferable to total length and total area. Also, by measuring cephalothorax length, some degree of comparability with length measurements of copepods in other works could be maintained. Length was measured using an algorithm which calculated the areal moments of inertia (length and width) with respect to the centroid of the object to be measured (for full details of the algorithm consult the IBAS 2000 Reference Manual (Kontron 1985)). Area was measured as the projected surface area covered by pixel units. For non-copepod taxa, total length and projected surface area were

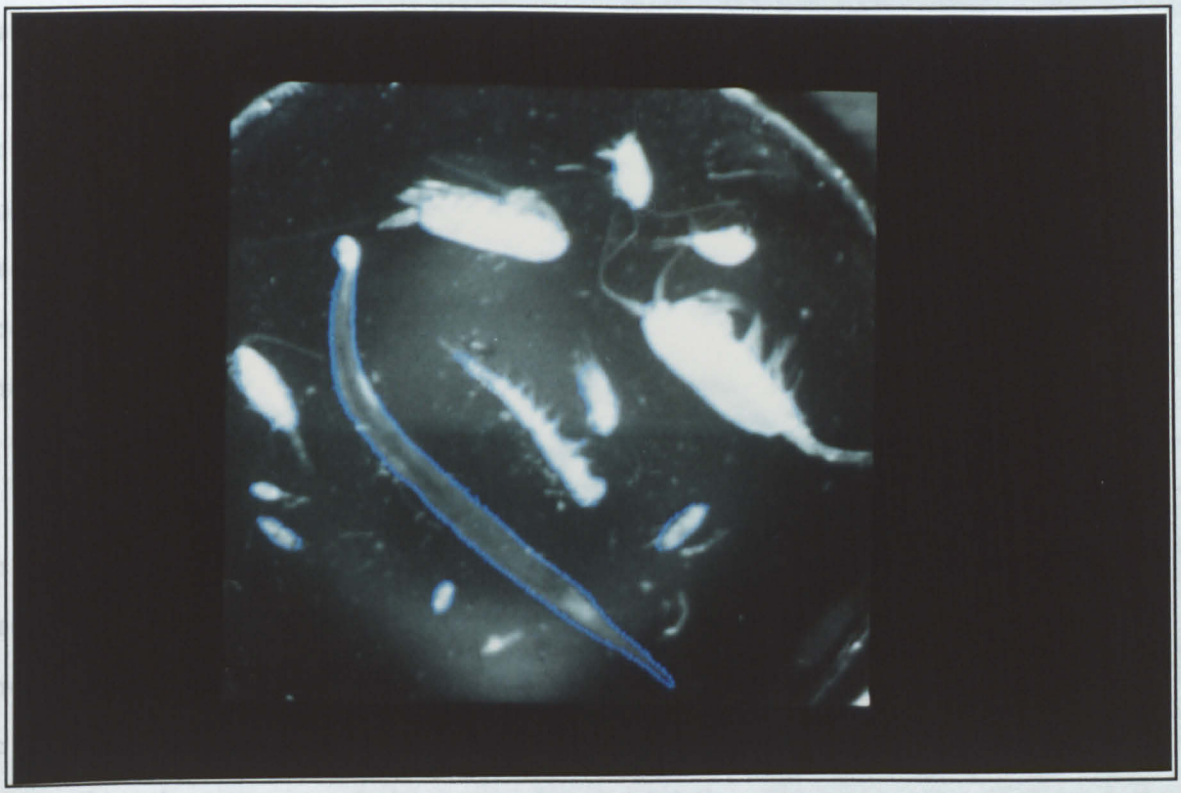


Figure 3.6 Photograph showing a typical zooplankton sample where the outlines of discriminated objects (shown in blue) have been superimposed onto the original image to check for agreement between the two.

measured for most species. Because many of these specimens were often curved, length measurements made through the centroid will not be as accurate as those obtained for the copepods. Figure 3.7 shows a typical zooplankton sample and the corresponding length and area measurements made for several representative groups. All measurements were converted to millimetres by means of a calibration scale entered at the start of the programme.

4) Data output:

Measurement data were stored in one of 19 data channels available on the Kontron; channels 1 to 18 were species specific while channel 19 was used for all remaining species. All data were stored on hard disk and later transferred to a Microvax computer for further analysis. Following measurement, all images were reduced to 1/4 screen size. Composite images consisting of four reduced images were stored on the Kontron hard disk and subsequently transferred to a Microvax using KERMIT. All images were permanently stored on TK50 CompacTape magnetic tape cartridges. A copy of the measuring programme used in this study can be found in Appendix 8.

Approximately 44,000 zooplankters were examined in the present study, most of which were processed using the image analyser. Exceptions were cyphonautes, bivalve larvae, cirripede and copepod nauplii, eggs, and zooplankton generally less than approximately 0.1mm in length. However, length measurements of all undamaged individuals belonging to these groups were made using a Wild-M5 dissecting microscope and a calibrated eyepiece micrometer. No size measurements of echinoderm larvae and appendicularians were made due to the generally poor condition of the specimens.

Figure 3.7 Photograph showing a typical zooplankton sample following discrimination and identification of individual objects prior to measurement. Areas were measured from the total number of pixels within each discriminated object. Length and width measurements are shown for a copepod (a and b), an euphausiid furcilia (c and d), and a chaetognath (e and f).

3.4 DATA ANALYSIS

3.4.1 Image Analysis Experiments

A number of experiments were undertaken to assess various aspects of the performance of the image analyser in the measurement of zooplankton. These experiments included the selection of a length measurement for use in the study and the comparison of measurements made using the image analyser with those obtained using a conventional microscopy method. A Wild M5 microscope was used in all experiments and all lengths refer to prosome length. Statistical analyses were conducted using either the SAS statistical package (SAS 1985), or the spreadsheet package Quattro Pro (Borland 1987). The methodology used in each experiment is outlined below.

1) Prosome length measurements were made for 100 *Pseudocalanus* C6 females using a microscope at 50X magnification, and three measurement functions MOMENT, FERET and DMAX using the image analyser at a magnification of about 15X. The objective was to select the best function for use in the present study and therefore all measurements were made on individual animals to enable paired comparisons. The MOMENT function has been previously described in section 3.3.2. The FERET function provides a measure of the calliper distance, i.e. the maximum distance between two parallel tangents, along the X and Y axis (Joyce-Loebl 1985); the larger of the two measurements is then taken to represent the object length. The DMAX function provides an estimate of the maximum object diameter based on 32 projections.

Prior to any analysis the frequency distribution of each variable was tested for normality using the Kolmogorov D statistic (SAS 1985). The results of this analysis showed that the FERET and microscope measurements were not normally distributed, even following a log transformation of the data. Therefore measurements from the microscope

and image analyser were compared using the nonparametric Wilcoxon's signed-ranks test (Sokal and Rohlf 1981). This test computes the difference between the paired measurements and tests the null hypothesis that the mean rank values are equal and therefore represent the same population (Walpole 1974). Measurements obtained using the microscope were taken to represent the true prosome length. Although there will be a degree of error associated with these measurements, this is the standard method used in collecting data of this type and thus forms the basis of the comparisons.

2) The objective of the second experiment was to examine whether variability associated with the image analyser was partly due to the lower magnification (ca. 15X) at which measurements were made. To address this question, paired measurements of 50 *Pseudocalanus* spp. C6 females were made using the microscope at a magnification of 12X and the MOMENT function, and compared with those made using the microscope at 50X magnification. The difference between measurements was then calculated for the three combinations: the image analyser and the microscope at 50X; the microscope at 12X and at 50X; and the image analyser and the microscope at 12X. In each case the mean rank value between each set of paired measurements was then tested for significance using a Wilcoxon's signed-ranks test.

3) The performance of the MOMENT function was also examined for copepods spanning a size range of approximately 3mm. Paired length measurements were made for 63 *Oithona* spp. and 27 *Calanus finmarchicus* using the MOMENT function and the microscope at 50X. In each case, a Wilcoxon's signed-ranks test was used to determine if the mean rank value was significantly different between paired measurements for each species.

4) Size-frequency distributions were also compared for individuals of *Calanus finmarchicus* using measurements obtained from the MOMENT function on the image analyser and the Wild microscope at 50X. Prosome

measurements were compared for a sample population containing the following mixture of copepodid stages and adults: 35·C1, 94·C2, 55·C3, 74·C4, 56·C5, 53·C6 females, and 53·C6 males, for a total number of 420 individuals. A Kolmogorov-Smirnov two-sample test (Sokal and Rohlf 1981) was used to determine whether the two frequency distributions were significantly different.

5) The variability in discrimination levels, i.e. the upper and lower grey level limits used to delimit an object from the surrounding background, was also examined for 27 individuals of *Calanus finmarchicus*, 151 *Pseudocalanus* spp., and 37 *Oithona* spp.. The objective of this exercise was to determine the feasibility of using fixed grey-level values in the discrimination step of the image analysis programme.

6) In the present study projected surface area measurements for all copepods were only for the body area as delimited by the prosome, (i.e., excluding all appendages, antennae, and the urosome and subsequently referred to as the prosome area). The relationship between the prosome area and the total surface area was examined for 44 *Calanus finmarchicus*, 151 *Pseudocalanus* spp., and 36 *Oithona* spp. The objective of this exercise was to examine the variability of this relationship over a range of animal sizes.

3.4.2 Total Zooplankton Numbers and Biomass

The total number of zooplankton, and the proportion of the sample in each size fraction collected, was determined for all stations sampled at 10 and 30m for each cruise (Appendices 9 and 10). The total number was calculated by adjusting the number of zooplankton collected in each size fraction (i.e. coarse, medium and fine) to the number per cubic meter and then summing these values to obtain the total number per cubic meter at each station.

During the May cruise, combined size fractions (i.e. coarse/medium

Table 3.2 Total zooplankton numbers and the percentage of the total sample comprised by each size fraction at stations where combined size fractions were collected in May 1986. Sample fractions for which numbers were estimated are shown in bold-face. Size fractions are designated as coarse: C; medium: M; fine: F. Δ is the difference between the total number calculated using the combined size fractions and that estimated using the separate size fractions. Δ% is the difference between the total numbers expressed as the percent increase relative to the total number calculated using the combined size fractions.

Station (Depth)	Coarse No (%)	Medium No (%)	Fine No (%)	Total No (C/FM)	Total No (C/M/F)	Δ	Δ%
FL8 (30m)	8.90 (0.06)	4720.13 (30.49)	**10750.32 (69.45)**	15417.52	15479.35	62	0.4
Y5 (10m)	4.51 (0.09)	**2268.39 (45.92)**	2666.67 (53.59)	4939.58*	4939.57	.01	.002
Y3 (30m)	32.50 (0.44)	1975.84 (26.60)	**5419.98 (72.96)**	7371.18	7428.32	57	0.8
Y3 (10m)	105.30 (1.37)	2853.66 (37.17)	**4719.38 (61.46)**	7593.30	7678.34	85	1.1
AB8 (30m)	12.75 (0.39)	689.28 (20.95)	**2587.57 (78.66)**	3258.14	3289.59	31	1.0
AB8 (10m)	5.58 (0.21)	1124.20 (43.13)	**1466.18 (56.48)**	2612.24	2595.96	16	0.6
AB38 (30m)	28.28 (0.28)	8994.03 (90.51)	**914.53 (9.20)**	2534.95	9756.84	7222	285
AB38 (10m)	46.46 (0.18)	22213.5 (86.93)	**3292.46 (12.89)**	10590.06	25187.14	14597	138
AB5 (30m)	10.32 (0.15)	2253.54 (32.18)	**4739.87 (67.68)**	6470.40	7003.73	533	8.2
AB5 (10m)	34.88 (0.70)	1476.09 (29.79)	**3444.34 (69.51)**	4922.99	4955.32	32	0.6

* CM/F size combination

or medium/fine fractions) were collected for 10 samples (Table 3.2). In order to estimate the proportion of each sample contained within the separate size fractions at these stations, the total number in each fraction was estimated as follows: for the coarse/medium fraction, the number for each species in the medium fraction was subtracted from the coarse/medium fraction to obtain the number of zooplankton in the coarse

fraction separately. For the medium/fine fractions, the number in the medium fraction was subtracted from the medium/fine fraction to give the number of zooplankton in the fine fraction. All subtractions were made according to species. If the number in the single medium fraction was greater than that in the combined fraction, then the species was regarded as being absent in the size fraction for which the total number was being estimated (i.e. the coarse or the fine). In Table 3.2, total numbers of zooplankton obtained using this method are compared with those calculated using only the combined samples. At eight of the ten stations, the numbers obtained using the method described above showed close agreement with those calculated using the combined size fractions. However, considerable disagreement in total numbers was observed at station AB38 for both the 10 and 30m sample. Upon examination of the samples, this difference was attributed primarily to large numbers of *Calanus* spp., and *Acartia clausi* Giesbrecht in the medium sized samples at that station. Furthermore, the low volume of water filtered for these samples (see Appendix 1) suggests that the large numbers of zooplankton may have resulted in some clogging of the medium filter at the time of collection. However, no adjustment to the raw data has been made with respect to zooplankton numbers at this station. Rather, coarse scales have been chosen in the presentation of abundance data which take into account this variability and appropriate transformations have been made prior to any applications of statistical analyses. Total zooplankton numbers calculated using the separate size fractions were used in the presentation of numerical abundance data and in all multivariate analyses.

Total zooplankton biomass and the proportion of each sample contained within each of the three size fractions were also determined for all samples collected as described in section 3.2.1. In some cases, the displacement volume of the separate sample exceeded that of the combined sample. When this occurred, the proportion of the biomass in

each of the size fractions could not be determined.

3.4.3 Multivariate Analysis

3.4.3.1 Choice of Technique

Numerous multivariate techniques are now routinely available for use in the analysis of ecological data (Gauch 1982). Although proponents of one technique versus another abound, the type of analysis used is largely dependent upon the specific objectives of the study, the nature of the data and, to a lesser degree, the facilities available.

In the present study the objectives in applying multivariate analyses were to elucidate coarse, or meso-, scale patterns among stations throughout the study area, to determine which species figured prominently in governing inter-station similarities and to relate the observed patterns to environmental variables. To achieve these objectives, two types of multivariate analysis were selected for use; a classification technique: hierarchical agglomerative clustering (HAC; see Everitt 1980; Gauch 1982), and an ordination technique: non-metric multidimensional scaling (MDS, see Kruskal and Wish 1978). The combined application of classification and ordination analyses in the examination of ecological data has been recommended by several workers (e.g. Gauch 1982; Field *et al.* 1982; Clarke 1988*a*). This is particularly the case in the analysis of pelagic community data where gradations in faunal assemblages are more likely to occur than abrupt shifts in species abundances and hence sample similarities (e.g. McKelvie 1985). In these instances hierarchical clustering may 'force' samples into discrete groupings which do not accurately reflect the real spatial pattern (Field *et al.* 1982). For this reason clustering is best used in conjunction with an ordination technique (Clarke 1988*a*). The combination of HAC and MDS has been successfully applied in the analysis of marine

benthic data sets (Field *et al.* 1982; Clarke 1988*a*). A brief discussion of the analyses used in the present study is given in the following two sections.

3.4.3.2 Hierarchical Agglomerative Clustering

Hierarchical agglomerative clustering (HAC) provides a graphical representation of community data by grouping together entities according to their degree of similarity. To begin, a similarity (or dissimilarity) matrix is calculated between all sample pairs, or among species. Numerous indices are available for use in constructing the similarity matrix (see Bloom 1981), the most common in ecological applications being the Bray-Curtis measure of similarity (Bray and Curtis 1957; see formula p. 82). This coefficient is generally preferred because it is not influenced by joint absences of species (Field and McFarlane 1968), and places more weight on abundant species than on rare ones (Field *et al.* 1982). It is regarded by Bloom (1981) to be the only similarity index to accurately reflect true similarity. Once the similarity matrix is constructed, entities (e.g. samples or species) can be clustered or linked using one of many available algorithms. In hierarchical clustering the choices include single linkage, complete linkage (sometimes referred to as nearest and furthest neighbour, respectively) or group average linkage (Gauch 1982). In general, the latter type of linkage is preferred, being intermediate between the two extremes, and groups of samples are fused according to the average level of similarity between all members of one group compared with that of another (Field *et al.* 1982; Clarke 1988*a*). In agglomerative, as opposed to divisive, clustering, entities are successively fused, proceeding from the most similar to the least similar and ending in a single cluster (Gauch 1982). Output is typically in the form of a dendrogram in which similar samples or species are clustered together. However, because clustering

proceeds until all entities have been fused, the level at which individual clusters are regarded as being separate entities is subjective (Field *et al.* 1982).

3.4.3.3 Non-metric Multidimensional Scaling

Non-metric multidimensional scaling (MDS) is one of many ordination techniques available that attempt to represent measures of sample or species similarities on a low-dimensional map, the distance between points reflecting the degree of similarity. A main difference between non-metric and metric ordination techniques lies in the underlying assumption of linearity. Metric ordination techniques, such as principal components analysis, assume that species respond in a linear fashion to underlying physical gradients (Fasham 1977; Prentice 1977). In non-metric techniques, such as MDS, only rank-order information is used in the ordination and the assumption of linearity is replaced with the weaker assumption of monotonicity (Prentice 1977; Gauch 1982). The latter assumption would seem preferable given that a species response to environmental gradients is typically nonlinear (Fasham 1977; Field *et al.* 1982; Kenkel and Orlóci 1986) and violation of this assumption can result in severe curvilinear distortion of the gradient in the two-dimensional ordination space (Fasham 1977).

Unlike multivariate analyses such as principle components analysis, which is based on eigenvalues (see Gauch 1982), MDS uses as its starting point a similarity or dissimilarity matrix. Thus by choosing an appropriate similarity measure, such as the Bray-Curtis measure of similarity (see formula p. 73), data editing to remove rare species or missing values is unnecessary (Field *et al.* 1982). This is especially useful in the examination of marine community data where species distributions are frequently patchy (Field *et al.* 1982). With MDS, similarities within data sets can be weighted proportionally in

order to favour more reliable samples (Field *et al.* 1982; Clarke 1988*a*) and measures of similarity in a variety of formats can be used (Kenkel and Orlóci 1986). MDS is an iterative process, the complete details of which are given by Kruskal and Wish (1978). There are six main steps in the process which are briefly summarised as follows:

1) The number of dimensions for the MDS plot is specified. This is usually two or three as higher dimensional plots are often difficult to interpret (Shepard 1974). It should be noted that unlike analyses based on principal components, each MDS configuration is specific for the number of dimensions selected. A two-dimensional solution does not represent the projection of a higher dimensional solution onto the two-dimensional plane (Field *et al.* 1982).

2) A starting map representing the spatial relationships among all samples is constructed. This can be either in the form of output from another ordination technique, or merely an arrangement of points chosen at random. The map is constructed in the number of dimensions specified.

3) The distances among station pairs (interpoint distances) as represented in the starting map are regressed against the corresponding similarity values in the data matrix using a monotonic (increasing) regression. Only information regarding the rank order of sample similarities is used.

4) A stress value is calculated to determine how accurately the map represents the true configuration of sample similarities. This value, sometimes referred to as the 'badness-of-fit' (Kruskal and Wish 1978), provides a guide to the degree of distortion which occurs when a multidimensional configuration is compressed into a few dimensions (Field *et al.* 1982). In general, stress values increase as the complexity of the data set (i.e. numbers of samples and/or species) increases and the dimensions of the plot decrease. A stress value of <0.05 generally indicates excellent spatial representation while a value >0.3 indicates representation comparable to that obtained from a

randomly generated plot (Clarke 1988*a*).

5) Sample positions on the map are perturbed in a direction of decreasing stress using a steepest descent algorithm.

6) Steps three to five are repeated until stress values are at their minimum.

MDS is conceptually simple in relation to other ordination techniques (Clarke 1988*a*). In the past, the main criticism has been that it is computationally demanding. Field *et al.* (1982) noted that computer time increased proportionally with n^2 and that sample number was limited to approximately 100. Gauch (1982) recommended use of the ordination technique detrended correspondence analysis (DCA) over MDS because, although they gave similar results, DCA used less computer time and memory (see Hill 1979; Hill and Gauch 1980 for details of DCA). However, with recent advances in computer capacity, this is no longer a serious constraint and programmes are now available to run MDS on a personal computer requiring only 512KB of memory. Furthermore, studies comparing MDS with a variety of metric ordination techniques have found MDS to give superior results in the ordination of simulated coenocline (Gaussian species response to a single environmental variable) and coenoplane (two environmental variables) data under many conditions (Fasham 1977; Kenkel and Orlóci 1986). Kenkel and Orlóci (1986) concluded that the earlier recommendation by Gauch and Hill (1980) and Gauch (1982), of DCA as the preferred multivariate technique, may have been premature.

However, the following points should be considered when using MDS as an ordination technique. MDS, like many other ordination methods, places more importance on coarse rather than fine scale distances (Clarke 1988*a*) and will therefore tend to best represent relationships between different groups of samples rather than that among samples within groups. In the present study this was not regarded as a problem since the objective was to elucidate coarse-scale patterns. More

importantly, being an iterative process, convergence to a global rather than a local minimum cannot be guaranteed. However, the possibility of obtaining a local minimum can be minimised by running the ordination with a number of different starting configurations. Field *et al.* (1982) maintain that if the same configuration solution with the same lowest stress value is obtained on a number of occasions, the optimal solution has almost certainly been found.

3.4.3.4 Data Editing and Details of Sample Analyses

Multivariate analyses were conducted using software developed at the Plymouth Marine Laboratory (see Clarke 1988*a* and *b*). These programmes have been developed primarily for use in a series of training workshops which focus on the statistical analysis and interpretation of marine community data and are organised through the Food and Agriculture Organisation of the United Nations (FAO), the Intergovernmental Oceanographic Commission (IOC) and the United Nations Environment Programme (UNEP).

All analyses were conducted using an IBM Personal System 2 micro-computer (model 55 SX) equipped with a maths-coprocessor. Species abundance data (no. m^{-3}) were entered using Microsoft Excel (Cobb and Mynhier 1988) in the form of a species-by-sample (i.e. station) matrix with a separate matrix for samples at 10 and 30m for each cruise. For the analysis of station data the following procedure was used:

1) Prior to analysis, taxa which might act to obscure the sample groupings due to the level of identification were removed from the data set. These were unidentified copepodids, all eggs, appendicularians, medusae, *Sagitta* spp., *Thysanoessa* spp., unidentified gelatinous zooplankton, copepod nauplii, unidentified euphausiid nauplii, calyptopis and furcilia, and unidentified harpacticoid copepods.

2) Abundance data for the remaining taxa were subjected to a

double square root transformation. This provided a more equal weighting between rare and common species whilst still generally retaining a greater contribution from the common species.

3) Similarity among samples was calculated using the Bray-Curtis coefficient (Bray and Curtis 1957):

$$S_{jk} = 100\ [1 - \frac{\sum_{i=1}^{p} |Y_{ij} - Y_{ik}|}{\sum_{i=1}^{p} (Y_{ij} + Y_{ik})}],$$

where Y_{ij} and Y_{ik} are the abundance of the i^{th} species in the j^{th} and k^{th} samples, for all species i=1,2,...,p. The resulting similarity matrix was then used in the multivariate analyses.

4) Station clusters were identified using hierarchical agglomerative clustering as described in section 3.4.3.2. above. All groups were fused using group-average linkage.

5) MDS was also used to identify station clusters using as input the similarity matrix created during the cluster analysis. To minimize the possibility of attaining a local rather than a global minimum, each MDS analysis was run using at least nine different starting configurations. A global minimum was accepted only when the same minimum stress value was achieved for at least three separate runs. In addition, results of the monotonic regression for each MDS run were checked to ensure that the regression was complete (indicated by a plateau in the stress value) and the corresponding Shepard diagram, a scatter plot of the actual distance d_{jk}, against the fitted distance $\hat{d}_{jk}$, was examined for scatter, evidence of a poor fit.

6) Stress for all analyses was measured using the equation:

$$\text{STRESS} = \Sigma_j \Sigma_k\ (d_{jk} - \hat{d}_{jk})^2\ /\ \Sigma_j \Sigma_k\ d^2_{jk}\ ,$$

where d_{jk} is the distance between samples j and k in the similarity

matrix and $\hat{d}_{jk}$ is the distance given by the fitted monotonic regression. This formula for measuring stress is known as 'formula 1' (Clarke 1988*a*). Stress values and configuration solutions were recorded for both two- and three-dimensional solutions. Although stress values were always higher for the two-dimensional solutions (see no.4 in section 3.4.3.3), the ordination plots, when combined with the results of the corresponding cluster analysis, still provided a reasonable picture of the inter-station relationships and did not significantly differ from the three-dimensional solutions. Only on two occasions did the two- and three-dimensional solutions differ noticeably with respect to station positioning and in each case the position of only one station was altered. In these instances both the two- and three-dimensional solutions are given. However, given the greater ease of interpretation for the two-dimensional plots, these configuration solutions are given for the remaining analyses.

3.4.3.5 Species Analyses

To determine which species most contributed to the station groups identified by the cluster and ordination analyses both descriptive and statistical analyses were used.

In the descriptive analysis, stations comprising each of the station groups, or subgroups if present, were combined and the relative abundances of species and taxa determined for the overall group. Only common species or taxa, i.e. those contributing $\geq$ 3% of the total fauna within each group, were considered in order of rank abundance. Although this is an indirect method of assessment, it would seem likely that species and taxa identified in this manner were important in determining the outcome of the multivariate analyses among at least some, if not all, of the stations.

In the statistical analysis, cluster and ordination techniques

similar to those used in analyzing for sample patterns (as outlined above in sections 3.4.3.2 and 3.4.3.3) were used in an attempt to ascertain which species contributed to the observed station clusters. Only species/taxa contributing ≥ 3% of the total fauna at at least one station were included, and prior to analysis species scores were standardised across all stations. Species groups were first identified on the dendrogram plot and these station clusters were used to delineate groups on the corresponding MDS plot. Species positions on the ordination plot were then replaced with the label of any station groups, taken from the corresponding sample analysis, in which the species abundance exceeded 3% at one or more stations within the group. Species oriented analysis, known as inverse or 'r' analysis, was used successfully by Field *et al.* (1982) in their examination of free-living nematodes in the Exe estuary. It is also discussed by Clarke (1988*a*).

3.4.3.6 Relationship to Environmental Variables

Once taxa contributing to the station clusters had been identified, the next step in the analysis was to determine any underlying physical parameters which could be influencing species distributions and therefore indirectly contributing to the observed patterns. In the present study the variables examined were temperature, salinity, phytoplankton biomass, measured as chlorophyll *a*, and total depth.

For this analysis environmental data files containing temperature, salinity, chlorophyll *a* and total depth, obtained from the CTD profiles, were compiled for all stations sampled at 10m and 30m during each cruise. Using the statistical package developed at Plymouth (see section 3.4.3.4) data for each variable were, in turn, superimposed onto the corresponding MDS station analysis. Each variable was represented by a specific symbol with the size reflecting its relative magnitude within

the range of values obtained for any given analysis. However, since symbol size was related to the range of sampled values, a small range could be displayed as a much larger gradient than it biologically represented. For this reason, and to allow for direct comparison among symbols for each variable across all plots, the following procedures were used for standardization. All values of temperature were plotted after setting the minimum and maximum values at 5°C and 10°C, respectively. All values of salinity were plotted using a range of between 31 and 36°/oo. In the case of chlorophyll *a*, the scale used was from between 0 to 1.30mg m^{-3}. Total depth values were plotted using a scale of between 0 and 275m. In all cases, variables were initially plotted using the original range of values and these were compared with those generated in the standardized manner. None of the plots obtained using standardization contradicted any trends observed in the initial plots. However, it is believed that using standardization more accurately reflected the scale of the environmental gradients, particularly in the case of temperature where the total range in values throughout the study area in May was only 2.5°C.

3.4.4 Biomass Partitioning

In addition to the estimates of total zooplankton biomass made at each station using displacement volumes (see section 3.2.1), estimates of biomass were made for individual zooplankters using the measurement data collected from the image analyser. Depending on the general shape of a given taxa, length and/or area measurements were incorporated into formulae in order to calculate individual biovolumes (Table 3.3). Although this provided only approximate values for some of the taxa collected, it is thought that reasonable estimates were obtained in most cases. Biovolumes were not calculated for fish larvae, gelatinous zooplankton, or unidentified specimens, all of which contributed

Table 3.3 Formulae used in the calculation of zooplankton biovolumes and the corresponding species and taxa with which each was used. All volumes assuming a spherical shape were calculated using the formula based on length; the alternative formula was used in the calculation of correction factors for taxa denoted by an * as explained in the text. N/A indicates formulae were not applicable. L denotes length; A denotes area; D denotes diameter.

Object Shape	Volume		Taxa
	Using Length	Using Area	
Cylinder	N/A	$\frac{\pi A^2}{4L}$	euphausiid furcillia and calyptopis; chaetognaths; decapod zoeae and megalopa; amphipods; polychaetes; mysids; ascidians
Prolate Spheroid	N/A	$\frac{8A^2}{3\pi L}$	all calanoid and cyclopoid copepods excluding *Oithona minuta*, *Paroithona parvula*; cyprids
Sphere	$\frac{\pi D^3}{6}$	$\frac{4A^{3/2}}{3\pi^{1/2}}$	*O.minuta*; *P.parvula*; crustacean and euphausiid eggs; euphausiid and cirripede nauplii; harpacticoid copepods; gastropods; *Podon leucartii*; cyphonautes; ostracods; copepod nauplii*; *Littorina littorea**; *Evadne nordmanni**

minimally to the overall biomass.

However, for copepod nauplii, *Evadne nordmanni* Lovén, and eggs of *Littorina littorea* (Linnaeus), biovolumes calculated as equivalent spherical volumes based on length measurements, appeared to result in disproportionately large values relative to the size distribution and abundance of the taxa. For *L. littorea*, values were halved because the eggs are typically sub-spherical. For the two remaining taxa, increased biovolumes arose primarily through using length, the only available measurement to estimate body surface area and subsequently biovolume. To adjust for this overestimate, biovolumes were calculated using the formulae for a sphere shown in Table 3.3 using animals in each taxa for which both length and area measurements were available. Biovolumes calculated in this manner were compared for 72 copepod nauplii and it

was found that on average the ratio between values calculated using areas versus lengths was 0.41 (i.e. for n=72, x=0.41 and sd=0.15). For *E. nordmanni*, a similar relationship was observed, and the ratio was 0.48 (i.e. for n=409, x=0.48 and sd=0.13). For both of these taxa all biovolumes were adjusted by multiplying the equivalent spherical volumes by the appropriate correction factor.

3.4.4.1 Between Cruises

Biomass partitioning on a coarse-scale was examined between cruises for collection at 10m and 30m. Biovolumes were calculated for all individuals, using the appropriate formulae. In this analysis individuals of *Calanus finmarchicus* and *C. helgolandicus* were grouped together with *Calanus* spp.. Individual biovolume measurements were adjusted for the subsample fraction examined and the volume of water filtered. This resulted in quantitative estimates of biovolume which could then be better related to the corresponding abundance data. In each case, total number and biovolume were expressed as $\log_{10}(x+1)$, where x was the combined number or biomass per litre, for taxa which individually contributed to make 95% of the total biomass during the March cruise and 99% during the May cruise; the higher value was chosen for the latter due to the predominance of *Calanus* spp. at that time. The remaining 5% and 1% of the biomass, respectively, was treated collectively and labelled as 'other'.

3.4.4.2 Within Cruises

A more detailed examination of biomass partitioning was conducted within cruises for taxa comprising each of the station groups identified by the multivariate analyses. For each station group, biovolumes were calculated for individual zooplankters using the method described above.

Biovolumes were then summed according to $\log_2$ size-classes for each individual taxon. Taxa within each station group were ranked in order of decreasing contribution to the total biomass within the group. Size spectra by biomass (hereafter referred to as biomass spectra) were then examined for those taxa which collectively comprised 95% of the total biomass for each station group. To account for the differing number of stations within each of the multivariate groups, and to make the biomass spectra among groups comparable, biovolumes were divided by the number of stations in the group so that mean values were used in the construction of all spectra.

Corresponding size spectra by abundance (hereafter referred to as abundance spectra) were also examined for each taxa for which the biomass spectrum was examined. Abundance spectra were constructed by summing the number of individuals occurring in each $\log_2$ size class according to taxon.

4. RESULTS

4.1 IMAGE ANALYSIS

4.1.1 Choice of Length Measurement

Prosome length measurements for 100 *Pseudocalanus* C6 females made using a Wild M5 microscope at 50X were compared with those obtained using three different measurement functions available on the image analyser (Table 4.1).

Table 4.1. Summary statistics for prosome length measurements made for 100 *Pseudocalanus* C6 females measured using a Wild M5 microscope at 50X and three separate measurement functions on the image analyser. SD is the sample standard deviation. %MEAN is the mean difference between the image analyser measurement and the corresponding microscope measurement expressed as a percentage of the microscope prosome length. Similarly, %MIN, %MAX and %RANGE are expressed as a percentage of the microscope length.

	MEAN	SD	%MEAN	%MIN	%MAX	%RANGE
MICROSCOPE	1.076	0.045	-	-	-	-
MOMENT	1.153	0.060	7.24	-6.98	15.52	22.50
FERET	1.056	0.098	-1.76	-22.56	10.84	33.40
DMAX	1.147	0.058	6.67	-6.27	15.10	21.37

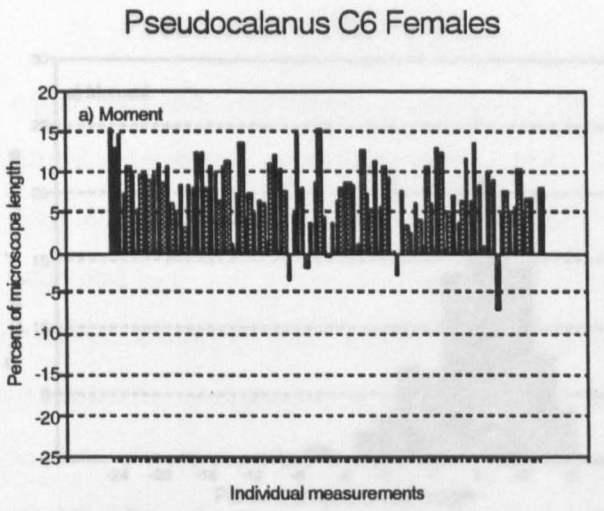
The statistics shown in Table 4.1 illustrate several differences between the three measurement functions examined for the image analyser. Both MOMENT and DMAX tended to overestimate the length of *Pseudocalanus* individuals with mean prosome lengths of 7.24 and 6.67%, respectively, greater than the corresponding microscope measurements. In contrast, the FERET measurement slightly underestimated the microscope values, with a mean of -1.76% prosome length. The Wilcoxon's signed-ranks test for

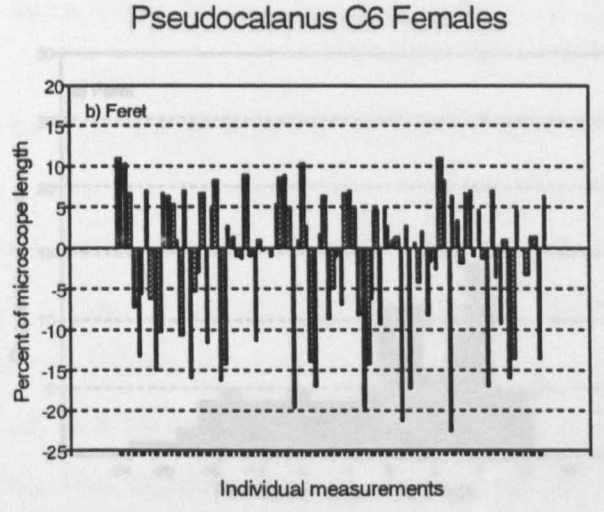
paired observations was used to determine whether the mean values obtained for each of the measurement pairs were significantly different. Both the MOMENT ($t_s = -7.876$, $p < 0.01$) and DMAX ($t_s = -8.331$, $p < 0.01$) functions were found to provide mean length measurements 8significantly different from those obtained using the microscope. Only the mean FERET measurement was found not to be significantly different from that obtained using the microscope ($T= -1.221$, $p > 0.05$).

Although the mean FERET measurement provided the closest approximation of the mean microscope measurement, this function also exhibited the highest range in individual measurements and thus the highest sample standard deviation (Table 4.1). Individual FERET measurements were as much as 23% less and up to 11% greater than corresponding microscope measurements, for a total range in values of about 34%. This was considerably larger than that observed for either the MOMENT or DMAX functions (Table 4.1).

The individual variability in length measurements for each of the methods is graphically displayed in Figure 4.1. This figure clearly illustrates the tendency for the MOMENT and DMAX functions to overestimate individual prosome length, while the FERET measurements were highly variable and displayed no consistent pattern. Combining the individual measurements into frequency distributions, expressed as percent deviation from microscope lengths, showed that both the MOMENT and DMAX functions peaked in the 8 to 10% class (Figure 4.2). In contrast, the deviation associated with the FERET measurement was distributed throughout the classes with no clear region of peak distribution.

These results indicated there were major differences among the three length measurements and the selection of a measurement will depend on the objectives of the study. For example, if the prime objective was to obtain an estimate of mean body length for use in estimating the rate of a size-dependent physiological parameter, then the FERET measurement





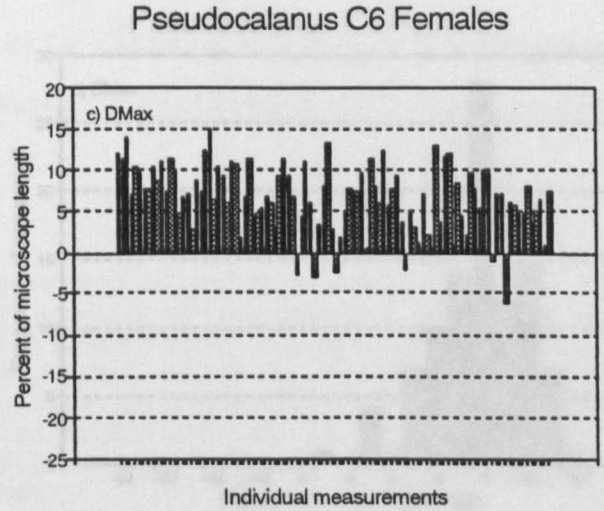


Figure 4.1 Comparison of individual prosome length measurements for 100 *Pseudocalanus* C6 females made using the Moment (a), Feret (b), and DMax (c), functions of the image analyser. All measurements are expressed as the percent deviation from corresponding microscope measurements at 50X.

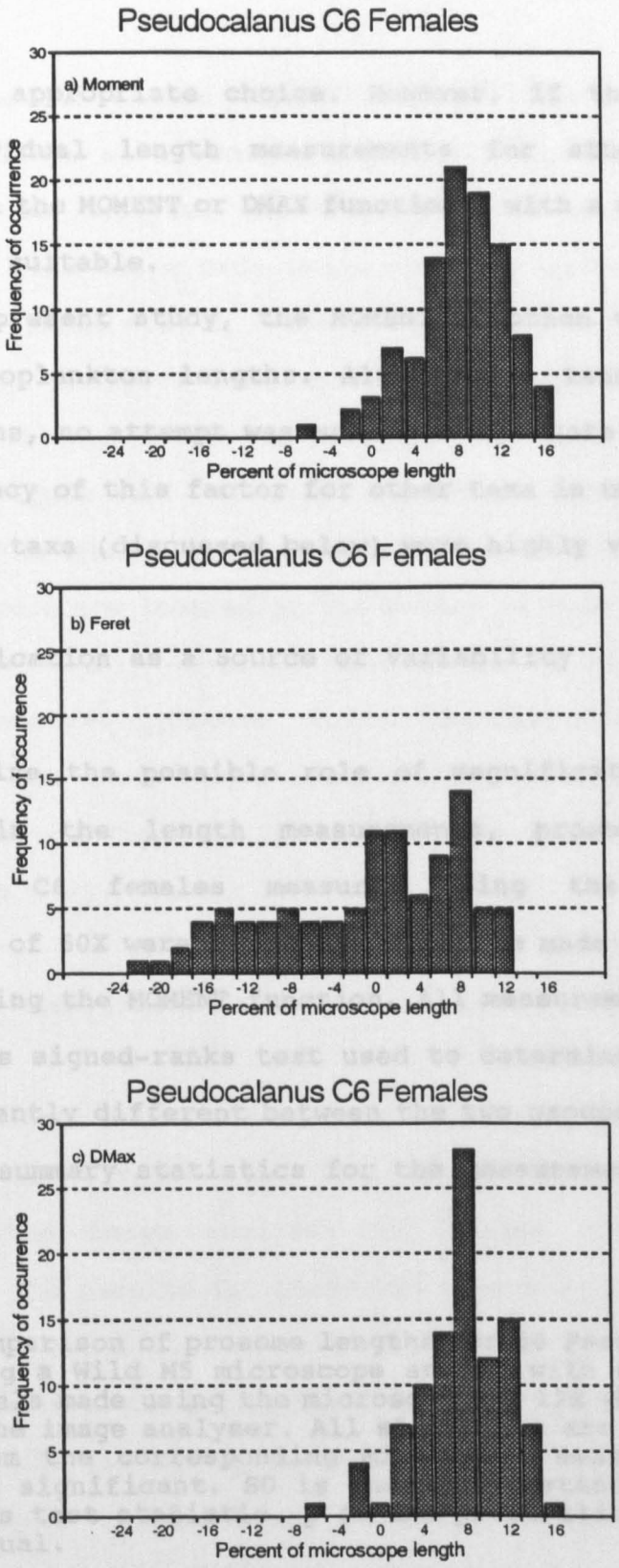


Figure 4.2 Frequency distributions of prosome length measurements for 100 *Pseudocalanus* C6 females made using the Moment (a), Feret (b), and DMax (c), functions of the image analyser. All measurements are expressed as percent deviation from corresponding microscope measurements at 50X.

would be the appropriate choice. However, if the objective was to provide individual length measurements for studies of population structure then the MOMENT or DMAX functions, with a smaller variability, would be more suitable.

In the present study, the MOMENT function was used to measure individual zooplankton lengths. Although it tended to overestimate prosome lengths, no attempt was made to compensate for this difference as the constancy of this factor for other taxa is unknown. Results from other copepod taxa (discussed below) were highly variable.

4.1.2 Magnification as a Source of Variability

To examine the possible role of magnification as a source of variability in the length measurements, prosome lengths for 50 *Pseudocalanus* C6 females measured using the microscope at a magnification of 50X were compared with those made using the microscope at 12X and using the MOMENT function. All measurements were paired and the Wilcoxon's signed-ranks test used to determine whether mean ranks were significantly different between the two groups. The results of the analyses and summary statistics for the measurement data are given in Table 4.2.

Table 4.2. Comparison of prosome lengths for 50 *Pseudocalanus* C6 females measured using a Wild M5 microscope at 50X with measurements for the same individuals made using the microscope at 12X (ML12X) and the MOMENT function on the image analyser. All statistics are expressed as percent deviation from the corresponding microscope measurements at 50X. ns signifies not significant. SD is the sample standard deviation. T_s is the Wilcoxon's test statistic. p is the probability that the mean rank values are equal.

	%MEAN	%SD	%MIN	%MAX	%RANGE	T_s	p>
MOMENT	3.08	4.55	-5.65	16.70	22.34	196	.01
ML12X	1.08	2.85	-3.56	7.67	11.23	434.5	ns

These results showed that the mean value of measurements made using a microscope at a reduced magnification, comparable to that at which the image analyser measurements were made, did not differ significantly from those made using the same microscope at the higher magnification (Table 4.2; $T_s = 434.5$). In comparison, measurements made using the image analyser remained significantly different from those made using the microscope at 50X. These results are graphically displayed in Figure 4.3. Although the MOMENT function still tended to overestimate the microscope length (Figure 4.3a) the majority of the measurements were now located in the region of 0 to 4% of the microscope length (Figure 4.3c), compared with about 8% for those individuals previously measured (Figure 4.2a). Measurements made using the microscope at the lower magnification tended to slightly overestimate the 'true' length (Figure 4.3b) with a mean value of about 1% (Figure 4.3c and Table 4.2).

4.1.3 Moment Measurements for Other Copepod Taxa

Paired length measurements were also made for a number of *Calanus finmarchicus* and *Oithona* spp. individuals in order to evaluate the accuracy of the image analyser for larger and smaller copepods, respectively. The results for these two taxa are summarised in Table 4.3 and Figures 4.4 and 4.5. These results showed that length measurements obtained using the image analyser were in good agreement with the corresponding microscope measurements for *Calanus finmarchicus*, but not for *Oithona* spp. (Table 4.3). The mean length measurement for *C. finmarchicus* using the MOMENT function was on average only slightly greater (1%; Table 4.3) than the corresponding microscope length, although individual measurements still tended to exceed the microscope values (Figures 4.4a and b). Using Wilcoxon's signed-ranks test for paired observations the mean values of *C. finmarchicus* length

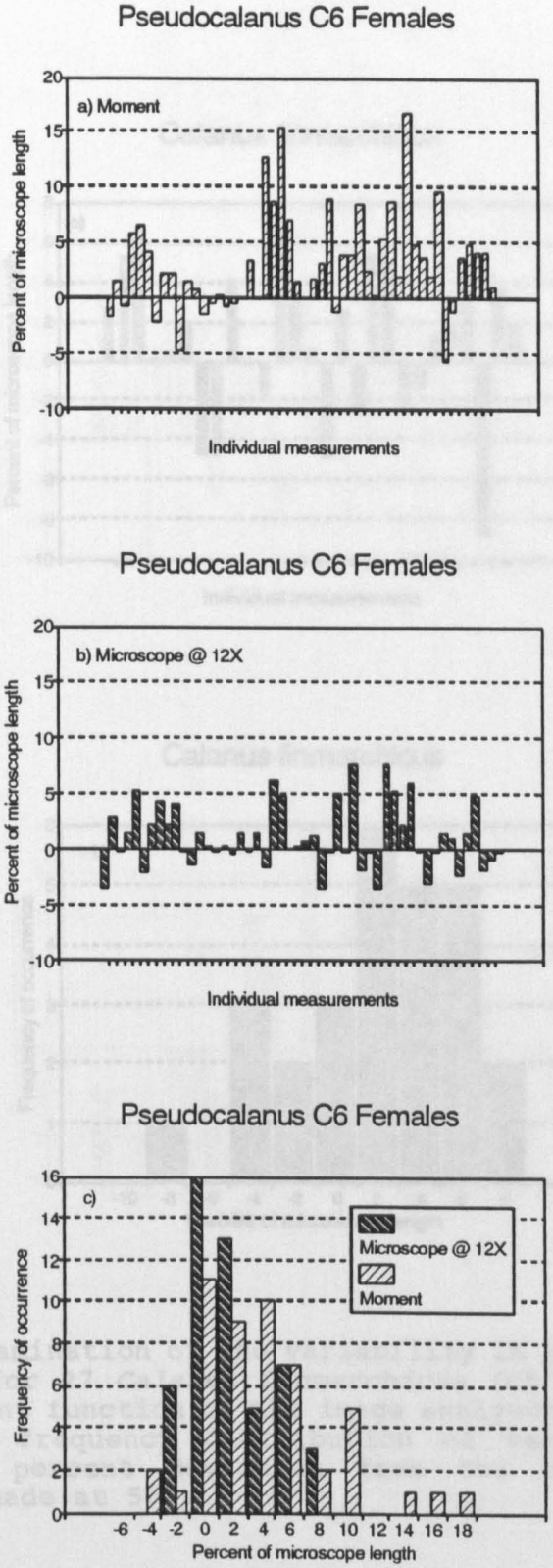
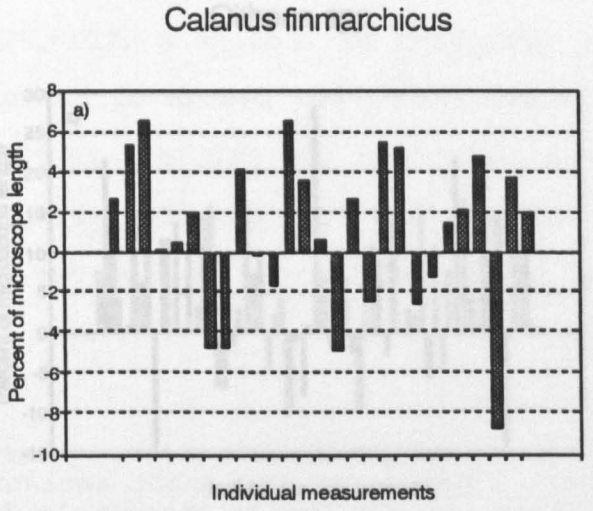


Figure 4.3 Comparison of prosome length measurements for 50 *Pseudocalanus* C6 females measured using a microscope at 50X with those made using the Moment function of the image analyser (a), and a microscope at 12X (b). The frequency distribution of the measurements, expressed as the percent deviation from the corresponding microscope measurements at 50X, is shown in (c).



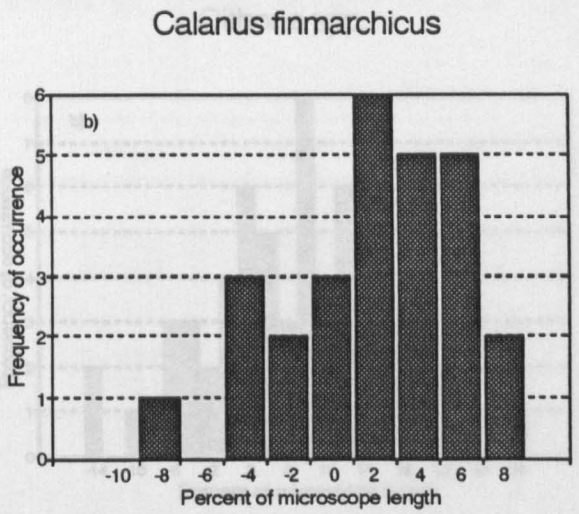


Figure 4.4 Examination of the variability in individual prosome length measurements for 27 *Calanus finmarchicus* (C5's and one C6 male) made using the Moment function of the image analyser. Individual variability (a), and the frequency distribution of variability (b), are both expressed as percent deviation from the corresponding microscope measurements made at 50X.

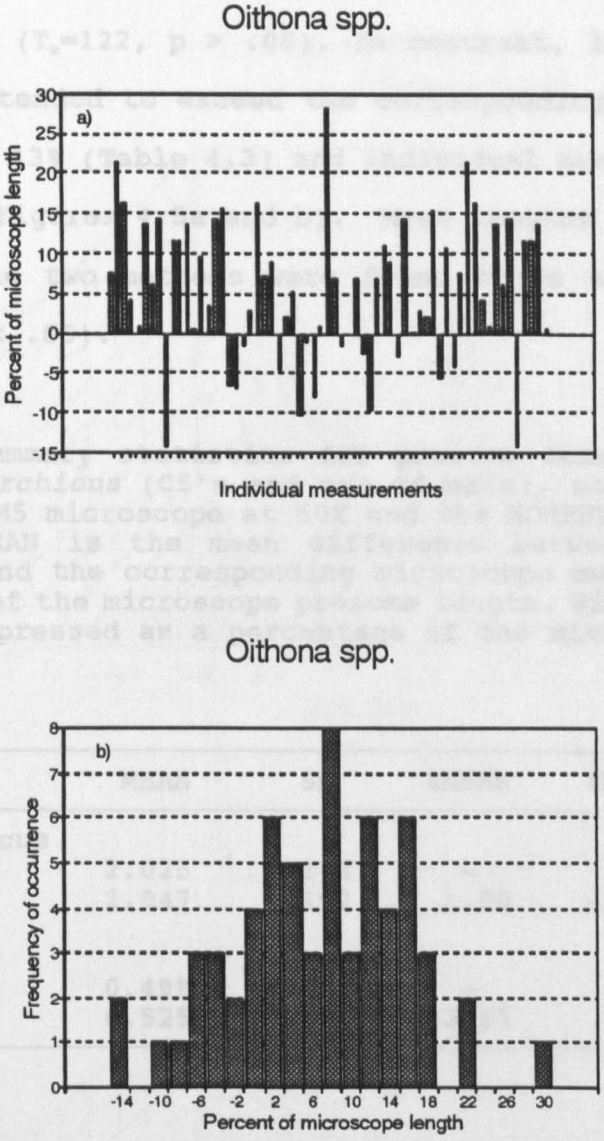


Figure 4.5 Examination of the variability in individual prosome length measurements for 63 *Oithona* spp. made using the Moment function of the image analyser. Individual variability (a), and the frequency distribution of variability (b), are both expressed as percent deviation from the corresponding microscope measurements made at 50X.

measurements made using these two methods were found not to differ significantly (T_s=122, $p > .05$). In contrast, length measurements for *Oithona* spp. tended to exceed the corresponding microscope lengths by an average of 13% (Table 4.3) and individual measurements showed great variability (Figures 4.5a and b). Mean lengths of paired measurements made using the two methods were found to be significantly different (T_s=2.403, $p < .05$).

Table 4.3. Summary statistics for prosome length measurements of 27 *Calanus finmarchicus* (C5's and one C6 male), and 63 *Oithona* spp. made using a Wild M5 microscope at 50X and the MOMENT function on the image analyser. %MEAN is the mean difference between the image analyser measurement and the corresponding microscope measurement expressed as a percentage of the microscope prosome length. Similarly, %MIN, %MAX and %RANGE are expressed as a percentage of the microscope length.

	MEAN	SD	%MEAN	%MIN	%MAX	%RANGE
C. finmarchicus						
MICROSCOPE	2.025	0.146	-	-	-	-
MOMENT	2.047	0.192	1.00	-8.74	6.51	15.25
Oithona spp.						
MICROSCOPE	0.498	0.094	-	-	-	-
MOMENT	0.525	0.106	13.61	9.00	20.5	29.5

4.1.4 Comparison of Size Frequency Distributions

A common objective in the collection of length measurements is to examine the size frequency distribution of individuals representing a natural population. To determine how accurately the image analysis measurements would portray such data, length measurements were made for individuals of *Calanus* ranging from copepodid stage 1 through to adults using both the image analyser and a microscope, and the size frequencies compared (Figure 4.6). In each case, the separation of the different developmental stages was clearly evident although there were differences

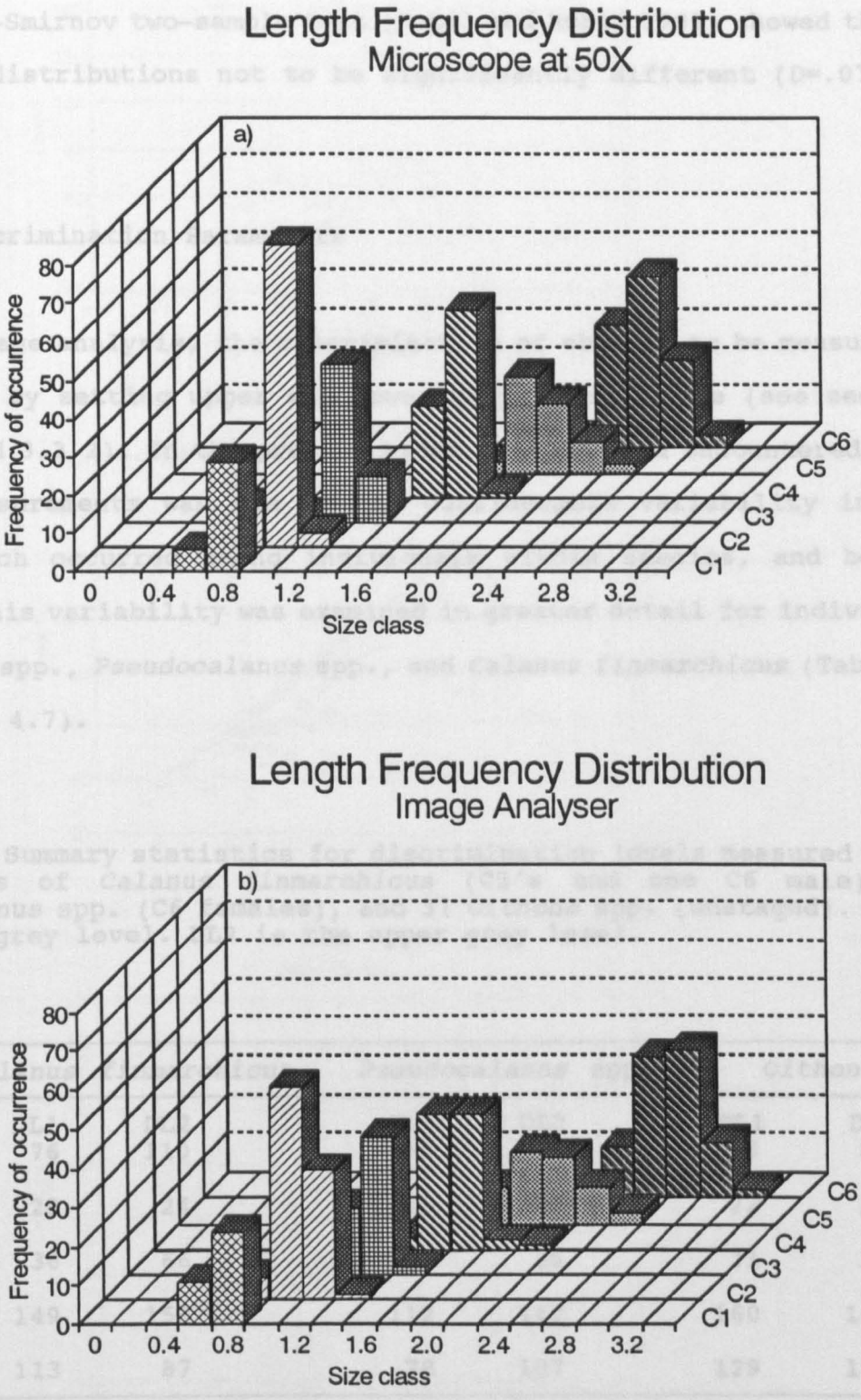


Figure 4.6 Comparison of prosome length frequency distributions for 420 *Calanus* spp. made using a microscope at 50X (a) and the Moment function of the image analyser (b).

in the distributions, particularly in the C2 stage. However, a Kolmogorov-Smirnov two-sample test (Sokal and Rohlf 1981) showed the two frequency distributions not to be significantly different ($D=.0738$, $p > .05$).

4.1.5 Discrimination Parameters

In image analysis, the discrimination of objects to be measured is determined by setting upper and lower grey-level limits (see sections 1.2.1.1 and 3.3.2). In the present study, one problem encountered while making measurements was due to the considerable variability in grey values which occurred among individuals within species, and between species. This variability was examined in greater detail for individuals of *Oithona* spp., *Pseudocalanus* spp., and *Calanus finmarchicus* (Table 4.4 and Figure 4.7).

Table 4.4. Summary statistics for discrimination levels measured for 27 individuals of *Calanus finmarchicus* (C5's and one C6 male), 151 *Pseudocalanus* spp. (C6 females), and 37 *Oithona* spp. (unstaged). DL1 is the lower grey level. DL2 is the upper grey level.

	Calanus finmarchicus		*Pseudocalanus* spp.		*Oithona* spp.	
	DL1	DL2	DL1	DL2	DL1	DL2
Mean	76	110	58	68	76	84
Std	28	24	15	22	22	20
Min	36	66	34	35	31	34
Max	149	153	112	142	160	163
Range	113	87	78	107	129	129

These results showed the considerable variability in grey values which occurred, both within and between species, when discrimination

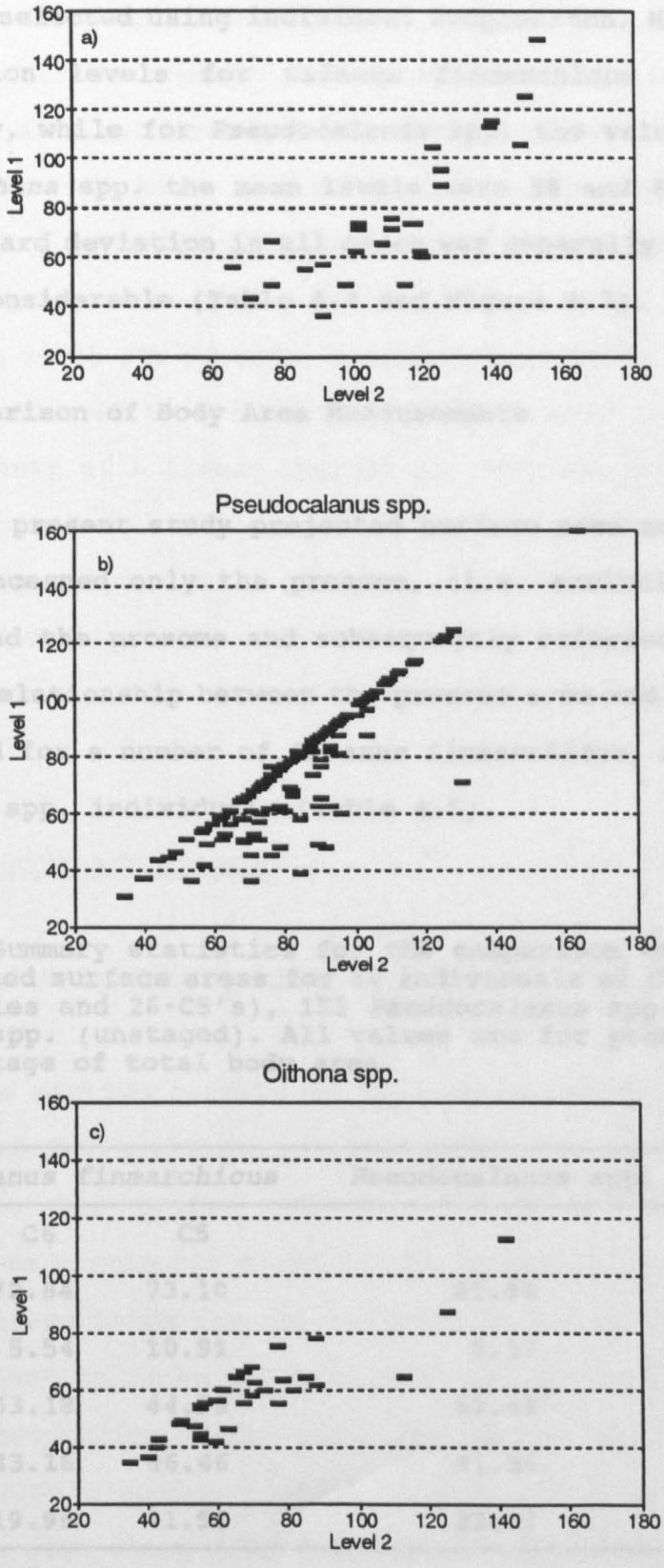


Figure 4.7 Examination of the variability in discrimination parameters for 27 *Calanus finmarchicus* (a), 151 *Pseudocalanus* spp. (b), and 37 *Oithona* spp. (c).

levels were selected using individual zooplankton. Mean lower and upper discrimination levels for *Calanus finmarchicus* were 76 and 110, respectively, while for *Pseudocalanus* spp. the values were 76 and 84, and for *Oithona* spp. the mean levels were 58 and 68 (Table 4.4). The sample standard deviation in all cases was generally high, and the range of levels considerable (Table 4.4 and Figure 4.7).

4.1.6 Comparison of Body Area Measurements

In the present study projected surface area measurements for all copepods concerned only the prosome, (i.e. excluding all appendages, antennae, and the urosome and subsequently referred to as the prosome area). The relationship between the prosome area and the total body area was examined for a number of *Calanus finmarchicus*, *Pseudocalanus* spp., and *Oithona* spp. individuals (Table 4.5).

Table 4.5. Summary statistics for the comparison of prosome and total body projected surface areas for 44 individuals of *Calanus finmarchicus* (18·C6 females and 26·C5's), 151 *Pseudocalanus* spp. (C6 females), and 36 *Oithona* spp. (unstaged). All values are for prosome area expressed as a percentage of total body area.

	Calanus finmarchicus		*Pseudocalanus* spp.	*Oithona* spp.
	C6	C5		
Mean	72.84	73.10	81.98	82.63
Std	5.54	10.91	5.17	7.16
Min	63.18	44.95	69.49	64.95
Max	83.16	86.46	91.56	98.98
Range	19.98	41.51	22.07	34.02

These results showed that, on average, the prosome area represented 73% of the total body area for *Calanus finmarchicus*, and 82%

and 83% for *Pseudocalanus* spp. and *Oithona* spp., respectively. The measurements for *C. finmarchicus* C5 copepodids were the most variable, with prosome area accounting for between 45 and 86% of the total surface area. In contrast, those for *C.finmarchicus* adult females showed the least variability ranging from 63 to 83% of the total body area. *Pseudocalanus* spp. showed the second least variability with prosome area ranging from 70 to 90% of total surface area, while values for *Oithona* spp. varied from 65 to 99% of total surface area (Table 4.5).

The result of a linear regression using the combined data sets is shown in Figure 4.8. Although there was some scatter of points evident among the larger individuals of *Calanus finmarchicus*, there was a strong linear relationship between prosome area and total area with $r^2 = 0.98$. The regression equation describing this relationship was $Y = -0.027X + 1.387$.

4.2 ZOOPLANKTON ASSEMBLAGES

4.2.1. Total Zooplankton Numbers and Biomass

In this section results of total zooplankton numbers and biomass are presented for stations sampled during the March and May cruises. Although the May cruise preceded the March cruise in terms of collection, as previously noted in the introduction, the March data are presented before those for May in order to provide a composite picture of the zooplankton fauna in early and late spring conditions. For each sample the proportion of the total number and biomass comprised by the coarse (>1000μm), medium (1000 - 330μm) and fine (330 - 180μm) size fractions is also shown (Figures 4.9 to 4.16). One problem encountered in the presentation of these results derives from the variable times of day for sample collection throughout the cruises. Given that zooplankton may undertake extensive diel vertical migrations (see Longhurst 1976a)

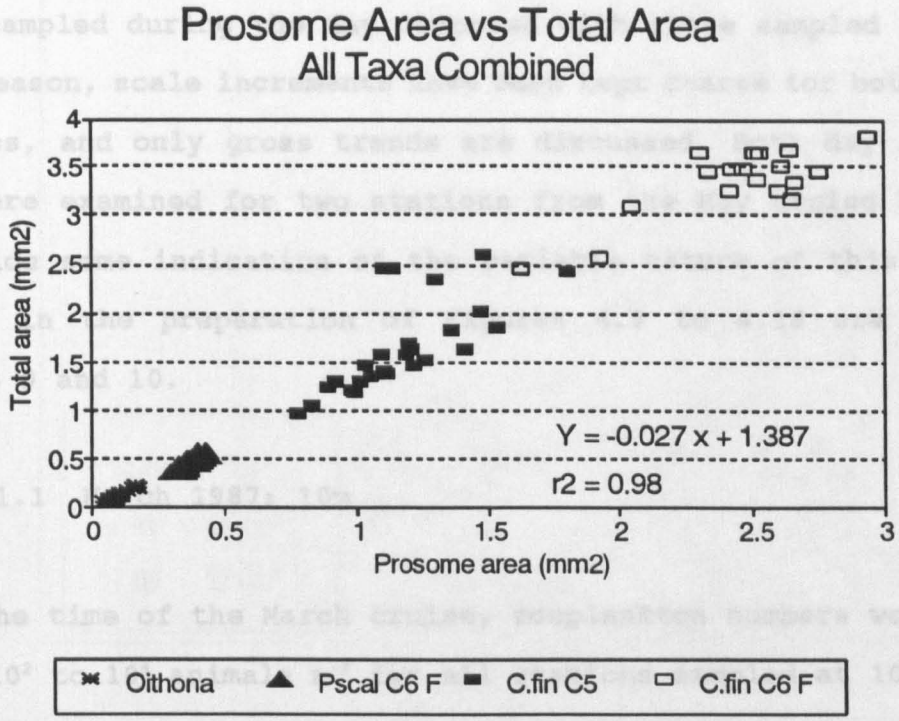


Figure 4.8 Comparison of prosome and total body projected surface area for 36 *Oithona* spp., 151 *Pseudocalanus* C6 females, and 44 *Calanus finmarchicus* (26 stage C5 and 18 C6 females).

total zooplankton numbers and biomass may be underestimated at those stations sampled during the day compared with those sampled at night. For this reason, scale increments have been kept coarse for both numbers and biomass, and only gross trends are discussed. Both day and night samples were examined for two stations from the May cruise and these data provide some indication of the variable nature of this problem. Data used in the preparation of Figures 4.9 to 4.16 are given in Appendices 9 and 10.

4.2.1.1 March 1987: 10m

At the time of the March cruise, zooplankton numbers were in the order of 10^2 to 10^4 animals m^{-3} for all stations sampled at 10m (Figure 4.9a). Numbers were generally higher, although variable, throughout the Firths of Lorn and Clyde and low on the Malin Shelf and in the North Channel. There was no clear trend between overall numbers and time of collection. Samples collected in March were fractionated into a medium (i.e. >330μm) and a fine component (see above); the coarse fraction was not collected separately. At 31 of the 33 (94%) stations sampled more than 50% of the fauna was comprised by the fine fraction (Figure 4.9b). On the Malin Shelf and in the Firth of Lorn, this component accounted for at least 84% of the total number collected in all samples. The fine fraction was also predominant in samples from the Firth of Clyde and North Channel, although there was an increase in the overall contribution of the medium fraction in these regions, particularly in the vicinity of Kilbrannan Sound. The medium fraction was dominant at only two stations: AB28 in the Firth of Clyde and A2 in the North Channel, where it accounted for 69% and 51% of the sample, respectively.

Corresponding measures of biomass were uniformly low throughout the study area at <1ml m^{-3} (Figure 4.10a). Although the fine fraction was again dominant, the medium fraction accounted for a considerable

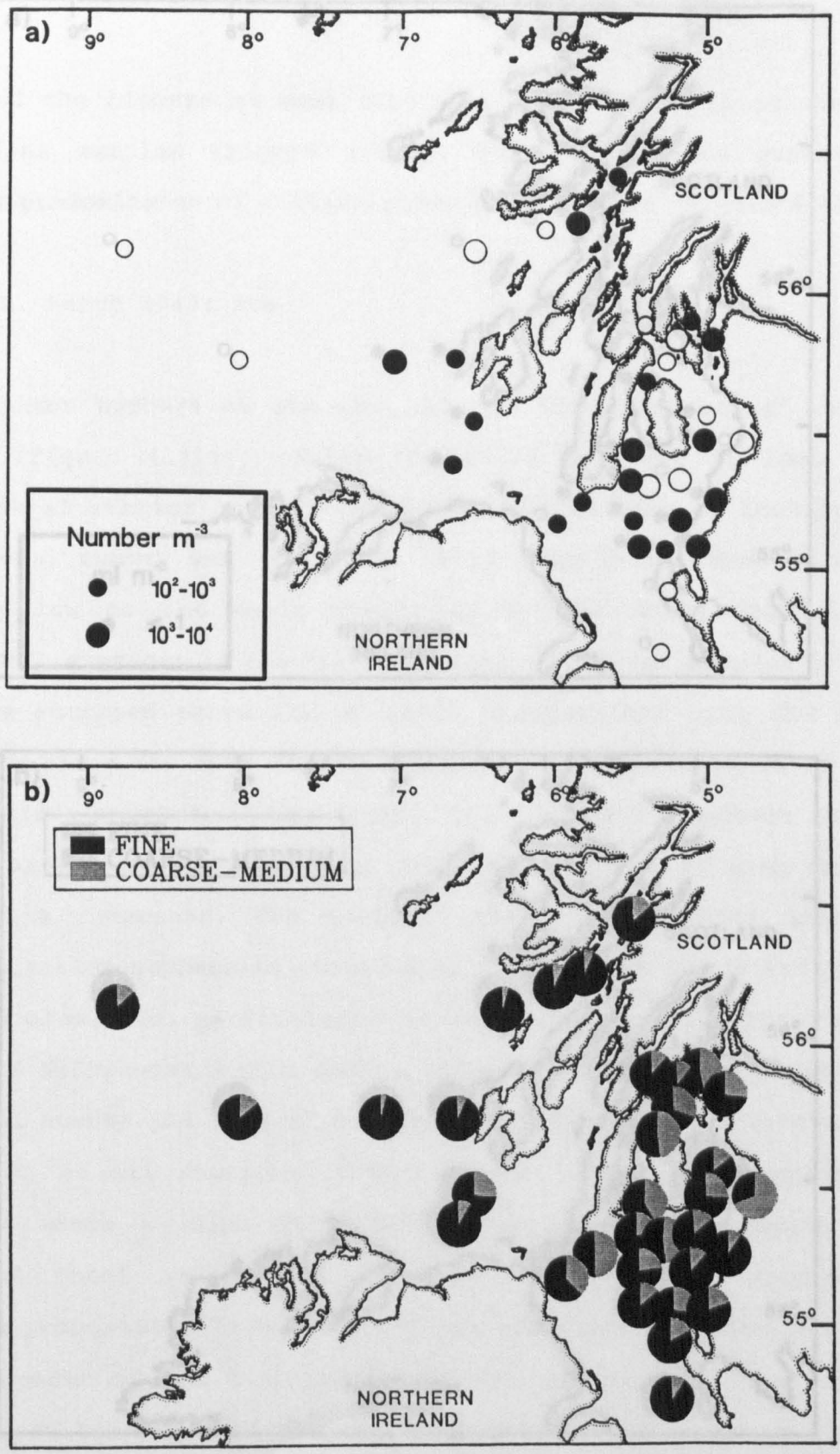


Figure 4.9 Total number of zooplankton collected at 10m in March 1987 (a), and the proportion in each size fraction (b). Empty circles represent stations sampled during day, solid circles represent stations sampled at night. Fine fraction is 330μm-180μm, coarse-medium fraction is >330μm.

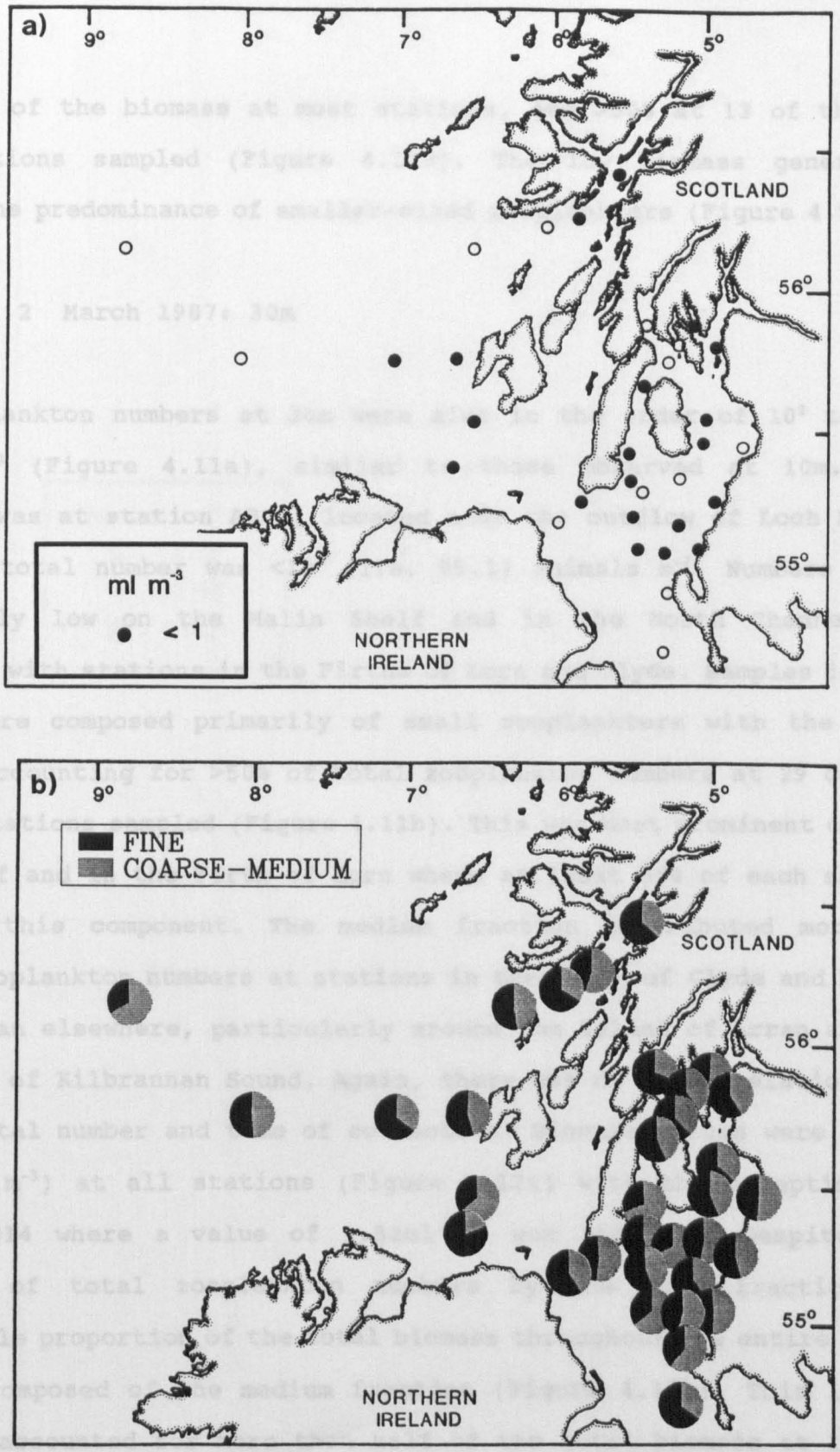


Figure 4.10 Total biomass of zooplankton collected at 10m in March 1987 (a), and the proportion in each size fraction (b). Empty circles represent stations sampled during day, solid circles represent stations sampled at night. Fine fraction is 330μm–180μm, coarse-medium fraction is >330μm.

proportion of the biomass at most stations, and >50% at 13 of the 33 (39%) stations sampled (Figure 4.10b). The low biomass generally reflects the predominance of smaller-sized zooplankters (Figure 4.9b).

4.2.1.2 March 1987: 30m

Zooplankton numbers at 30m were also in the order of 10^2 to 10^4 animals m^{-3} (Figure 4.11a), similar to those observed at 10m. One exception was at station AB38, located near the outflow of Loch Fyne, where the total number was $<10^2$ (i.e. 95.1) animals m^{-3}. Numbers were consistently low on the Malin Shelf and in the North Channel in comparison with stations in the Firths of Lorn and Clyde. Samples in all regions were composed primarily of small zooplankters with the fine fraction accounting for >50% of total zooplankton numbers at 29 of the 32 (91%) stations sampled (Figure 4.11b). This was most prominent on the Malin Shelf and in the Firth of Lorn where at least 86% of each sample comprised this component. The medium fraction contributed more to overall zooplankton numbers at stations in the Firth of Clyde and North Channel than elsewhere, particularly around the Island of Arran and in the region of Kilbrannan Sound. Again, there was no clear relationship between total number and time of collection. Biomass values were again low (<1ml m^{-3}) at all stations (Figure 4.12a) with the exception of station AB14 where a value of 1.53ml m^{-3} was recorded. Despite the dominance of total zooplankton numbers by the fine fraction, a considerable proportion of the total biomass throughout the entire study area was composed of the medium fraction (Figure 4.12b). This larger component accounted for more than half of the total biomass at 16 out of 30 (53%) stations examined with two stations having equal proportions of the fine and medium fractions. At station AB14 where the highest value was recorded, 89% of the sample was made up by the medium fraction. However, at other stations where much of the biomass was

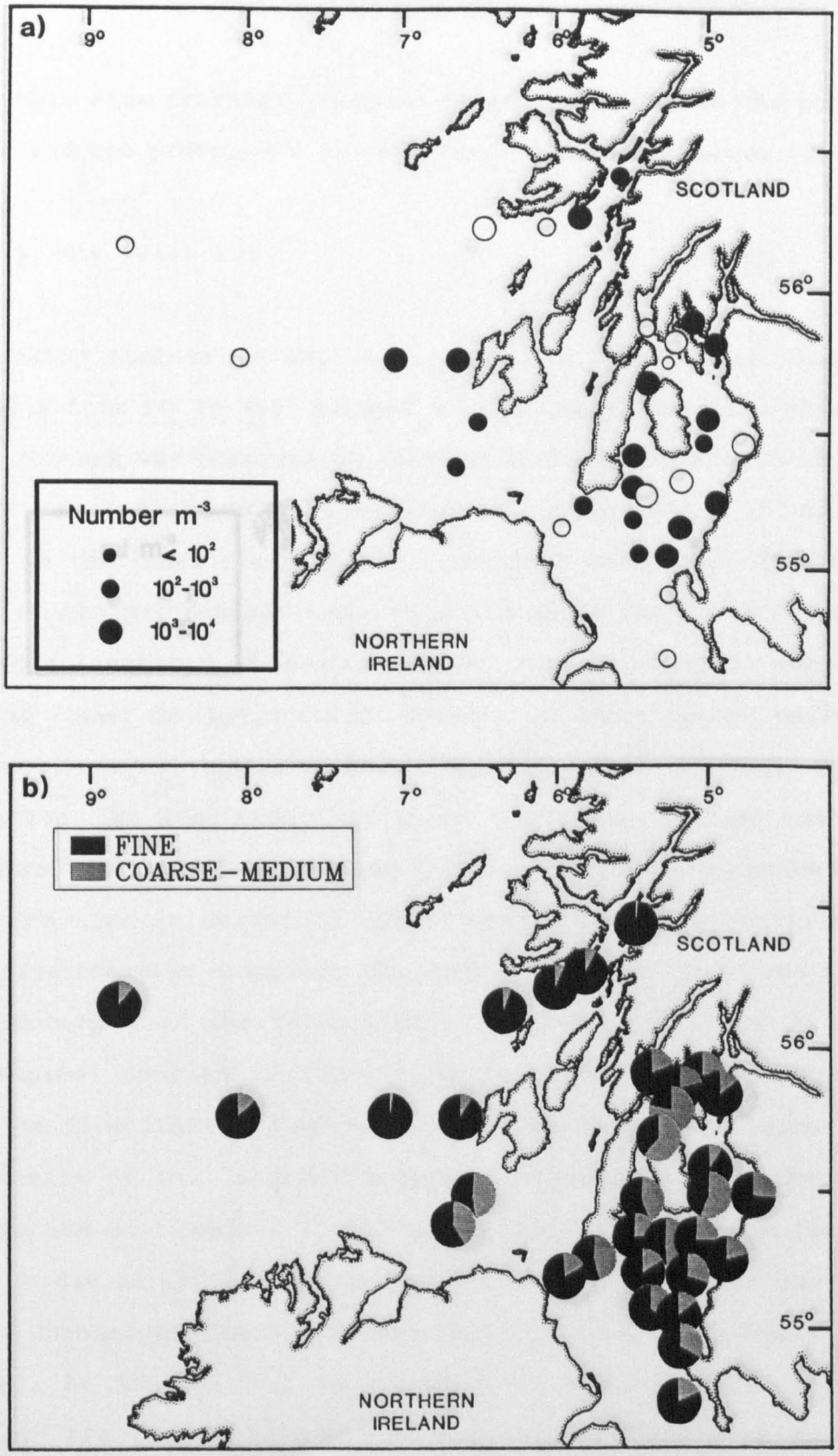


Figure 4.11 Total number of zooplankton collected at 30m in March 1987 (a), and the proportion in each size fraction (b). Empty circles represent stations sampled during day, solid circles represent stations sampled at night. Fine fraction is 330μm-180μm, coarse-medium fraction is >330μm.

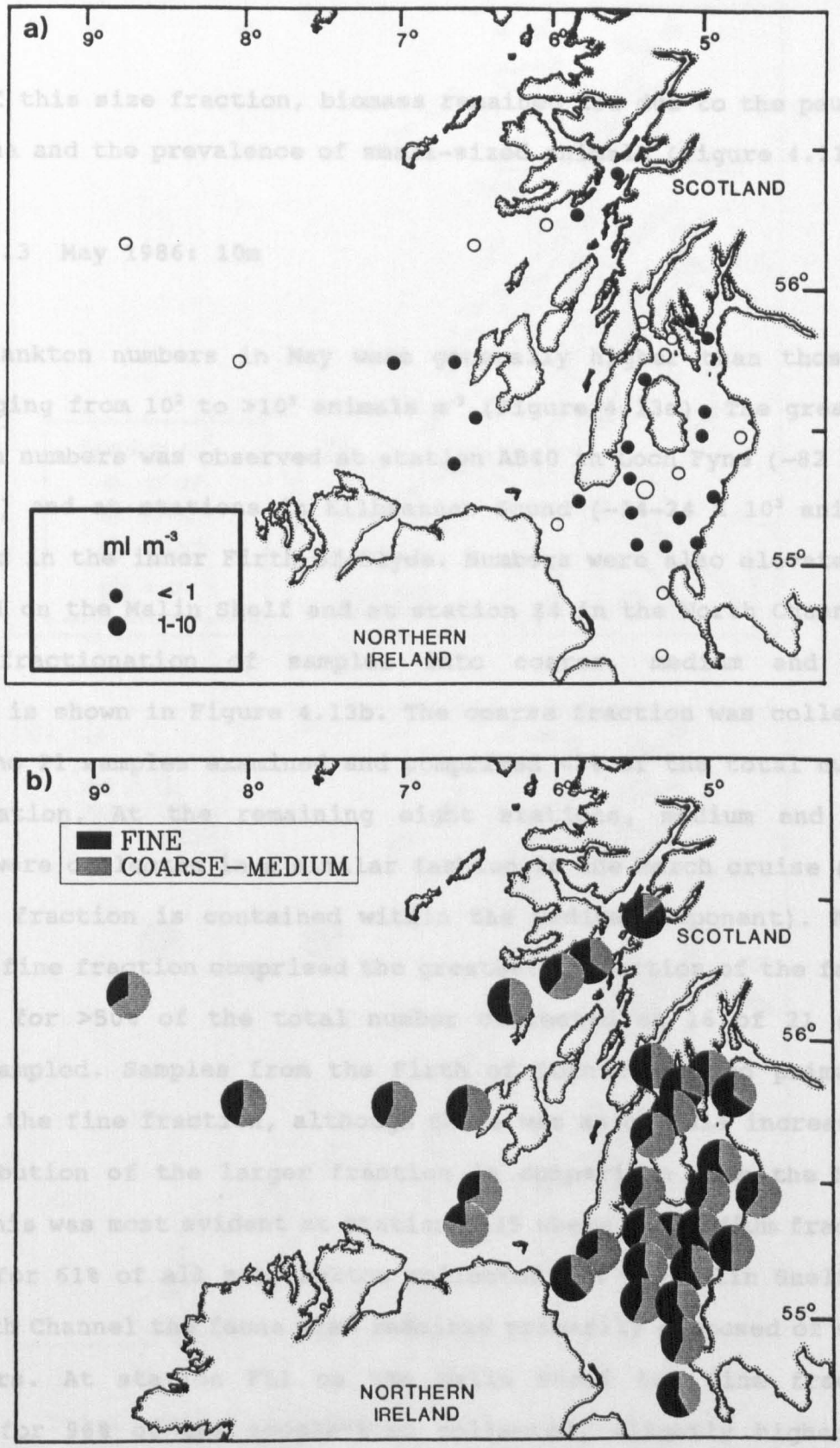


Figure 4.12 Total biomass of zooplankton collected at 30m in March 1987 (a), and the proportion in each size fraction (b). Empty circles represent stations sampled during day, solid circles represent stations sampled at night. Fine fraction is 330μm-180μm, coarse-medium fraction is >330μm.

composed of this size fraction, biomass remained low due to the paucity of the fauna and the prevalence of small-sized animals (Figure 4.11b).

4.2.1.3 May 1986: 10m

Zooplankton numbers in May were generally higher than those in March, ranging from 10^2 to $>10^5$ animals m^{-3} (Figure 4.13a). The greatest increase in numbers was observed at station AB40 in Loch Fyne (~82 X 10^4 animals m^{-3}) and at stations in Kilbrannan Sound (~14-24 X 10^3 animals m^{-3}) located in the inner Firth of Clyde. Numbers were also elevated at station FL1 on the Malin Shelf and at station Z4 in the North Channel.

The fractionation of samples into coarse, medium and fine components is shown in Figure 4.13b. The coarse fraction was collected at 13 of the 21 samples examined and comprised <2% of the total number at any station. At the remaining eight stations, medium and fine fractions were collected in a similar fashion to the March cruise (i.e. the coarse fraction is contained within the medium component). As in March, the fine fraction comprised the greatest proportion of the fauna, accounting for >50% of the total number collected at 16 of 21 (76%) stations sampled. Samples from the Firth of Lorn contained primarily animals in the fine fraction, although there was an overall increase in the contribution of the larger fraction in comparison with the March samples. This was most evident at station FL15 where the medium fraction accounted for 61% of all zooplankton collected. On the Malin Shelf and in the North Channel the fauna also remained primarily composed of small zooplankters. At station FL1 on the Malin Shelf the fine fraction accounted for 96% of the zooplankton collected, slightly higher but comparable to values on the shelf at 10m in March (Figure 4.9b). In the Firth of Clyde, conditions were variable with the medium fraction accounting for anywhere between 12.5% (station AB3A) and 96% (station AB40) of the total zooplankton fauna. In general, the medium fraction

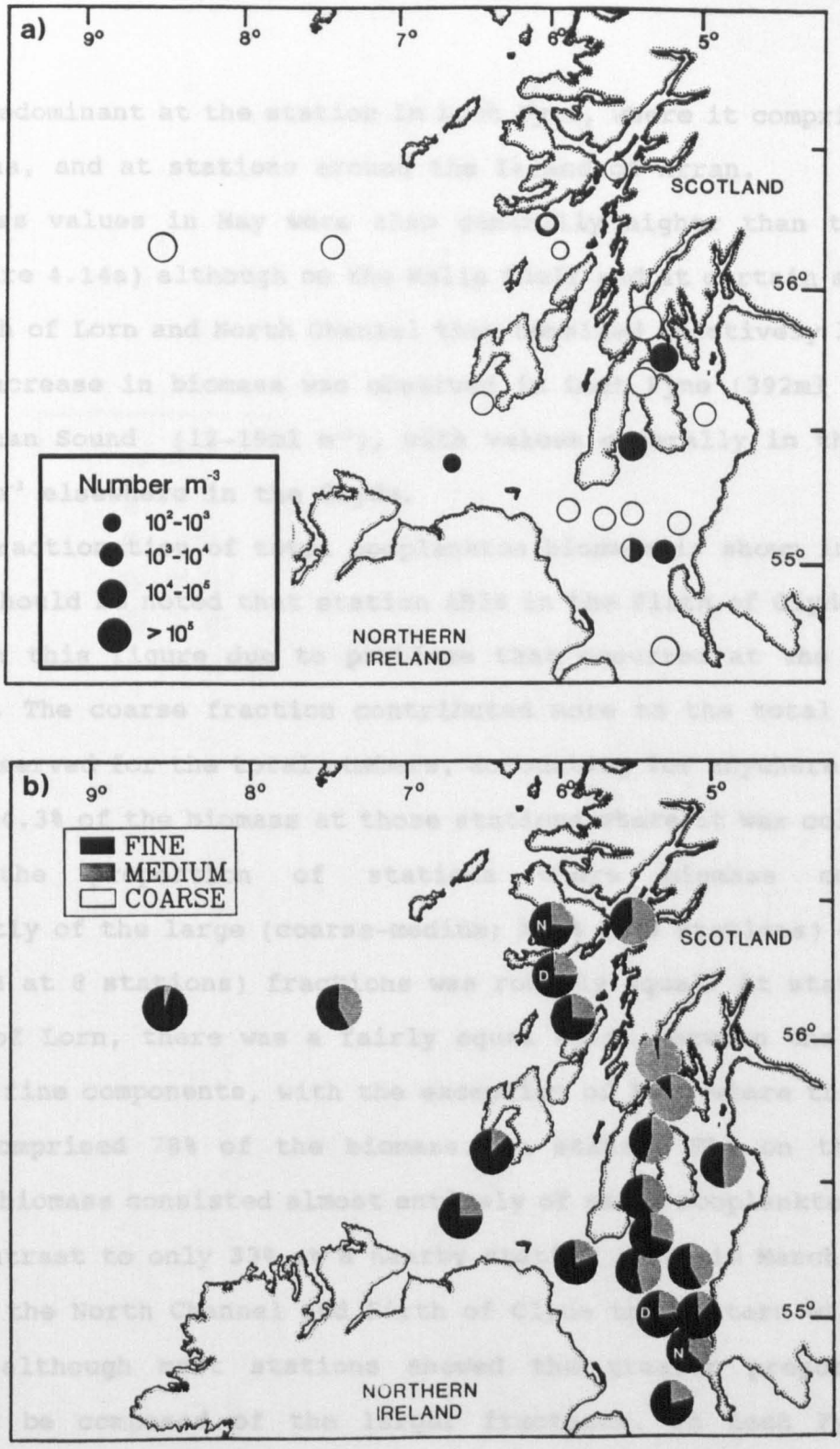


Figure 4.13 Total number of zooplankton collected at 10m in May 1986 (a), and the proportion in each size fraction (b). Empty circles represent stations sampled during day, solid circles represent stations sampled at night. Where values for total number have been superimposed, this indicates the station was sampled during both day and night. A black and white symbol indicates the same value was obtained for both day and night samples. Fine fraction is 330μm-180μm, medium fraction is 1000μm-330μm, and coarse fraction is >1000μm. For day and night samples representing size fractionation (b), the day sample (D) is shown on the station location and the night sample (N) either above or below.

was most predominant at the station in Loch Fyne, where it comprised 96% of the fauna, and at stations around the Island of Arran.

Biomass values in May were also generally higher than those in March (Figure 4.14a) although on the Malin Shelf and at certain stations in the Firth of Lorn and North Channel they remained relatively low. The greatest increase in biomass was observed in Loch Fyne (392ml m^{-3}) and in Kilbrannan Sound (12-19ml m^{-3}), with values generally in the range of 1-10ml m^{-3} elsewhere in the Clyde.

The fractionation of total zooplankton biomass is shown in Figure 4.14b. It should be noted that station AB38 in the Firth of Clyde is not included in this figure due to problems that occurred at the time of collection. The coarse fraction contributed more to the total biomass than was observed for the total numbers, accounting for anywhere between 0.05% and 14.3% of the biomass at those stations where it was collected. Overall, the proportion of stations where biomass consisted predominantly of the large (coarse-medium; >50% at 9 stations) or small (fine; >50% at 8 stations) fractions was roughly equal. At stations in the Firth of Lorn, there was a fairly equal split between the coarse-medium and fine components, with the exception of FL15 where the medium fraction comprised 78% of the biomass. At station FL1 on the Malin Shelf, the biomass consisted almost entirely of small zooplankters (i.e. 96%) in contrast to only 33% at a nearby station (FL0) in March (Figure 4.10b). In the North Channel and Firth of Clyde the pattern was highly variable, although most stations showed the greater proportion of biomass to be composed of the larger fractions. In Loch Fyne this fraction accounted for 96% of the total biomass collected.

4.2.1.3.1 Comparison of Day and Night Collections

Day and night collections were made at two stations in May 1986: FL12 located midway in the Firth of Lorn, and station Y3 located at the

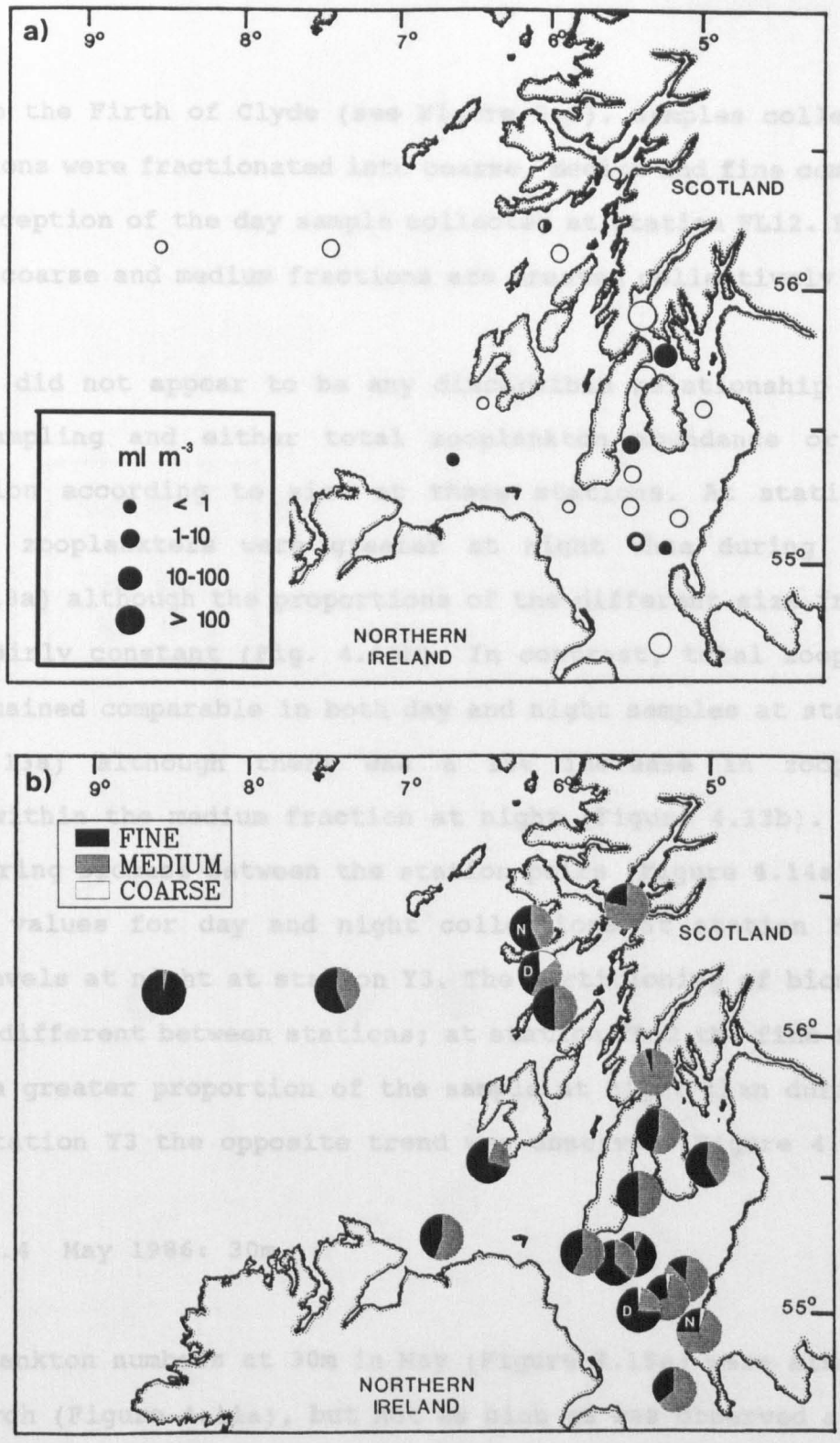


Figure 4.14 Total biomass of zooplankton collected at 10m in May 1986 (a), and the proportion in each size fraction (b). Empty circles represent stations sampled during day, solid circles represent stations sampled at night. Where values for total number have been superimposed, this indicates the station was sampled during both day and night. A black and white symbol indicates the same value was obtained for both day and night samples. Fine fraction is 330μm-180μm, medium fraction is 1000μm-330μm, and coarse fraction is >1000μm. For day and night samples representing size fractionation (b), the day sample (D) is shown on the station location and the night sample (N) either above or below.

entrance to the Firth of Clyde (see Figure 3.1). Samples collected at these stations were fractionated into coarse, medium and fine components with the exception of the day sample collected at station FL12. For this reason the coarse and medium fractions are treated collectively at this station.

There did not appear to be any discernible relationship between time of sampling and either total zooplankton abundance or sample fractionation according to size at these stations. At station FL12 numbers of zooplankters were greater at night than during the day (Figure 4.13a) although the proportions of the different size fractions remained fairly constant (Fig. 4.13b). In contrast, total zooplankton numbers remained comparable in both day and night samples at station Y3 (Figure 4.13a) although there was a 15% increase in zooplankton abundance within the medium fraction at night (Figure 4.13b).

Comparing biomass between the station pairs (Figure 4.14a) showed comparable values for day and night collections at station FL12 and elevated levels at night at station Y3. The partitioning of biomass was also quite different between stations; at station FL12 the fine fraction comprised a greater proportion of the sample at night than during day, while at station Y3 the opposite trend was observed (Figure 4.14b).

4.2.1.4 May 1986: 30m

Zooplankton numbers at 30m in May (Figure 4.15a) were also higher than in March (Figure 4.11a), but not as high as was observed at 10m in May (Figure 4.13a). Numbers were generally in the order of 10^3 to 10^4 animals m^{-3} with slightly higher (10^4 to 10^5) values occurring at station Z4 in the North Channel, AB17 in Kilbrannan Sound, and station FL8 in the outer Firth of Lorn (Figure 4.15a). The lowest abundances of 10^2 to 10^3 were recorded for stations E2 and the day sample at station FL12.

Numerically, much of the fauna was contained within the fine

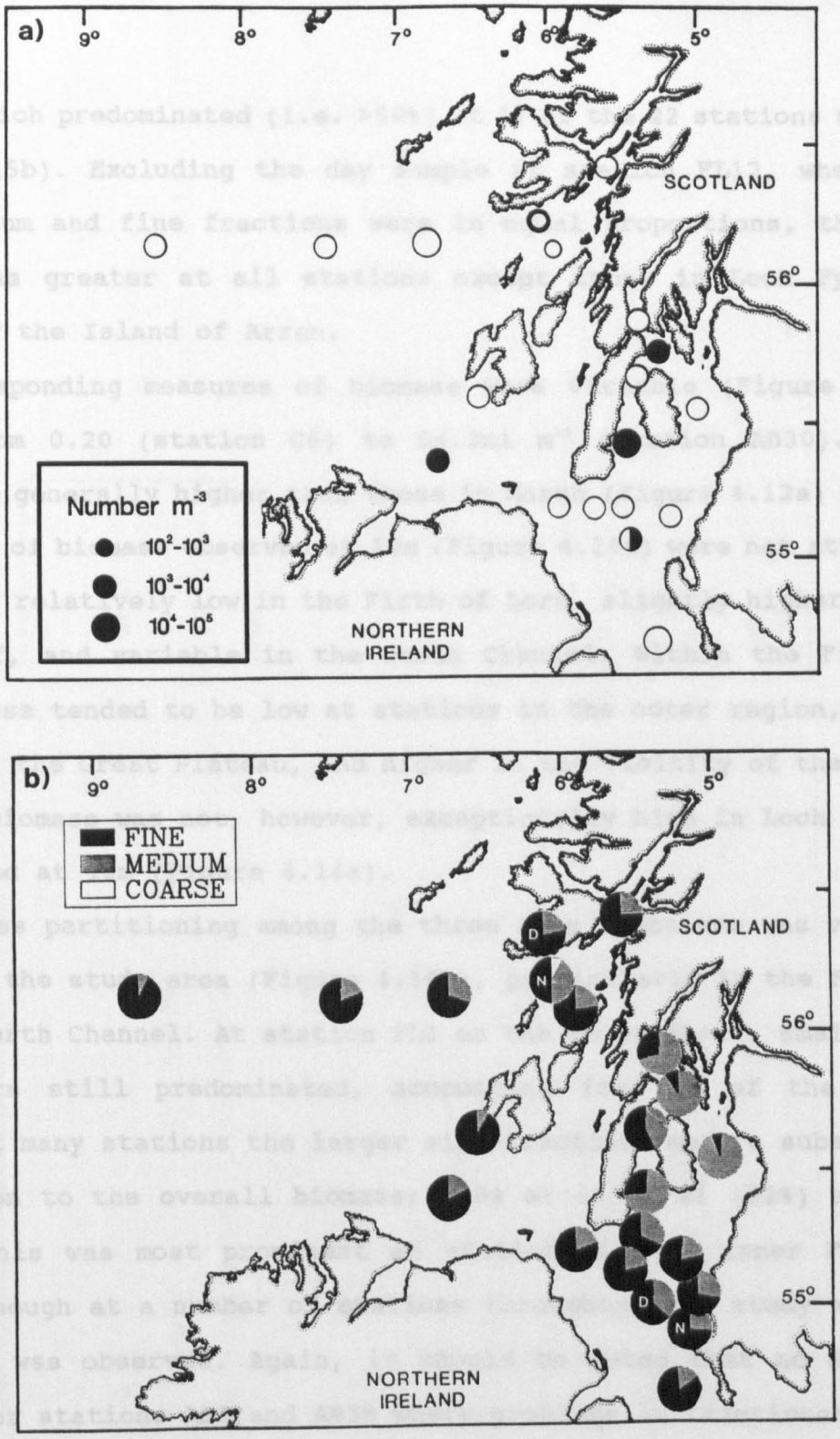


Figure 4.15 Total number of zooplankton collected at 30m in May 1986 (a), and the proportion in each size fraction (b). Empty circles represent stations sampled during day, solid circles represent stations sampled at night. Where values for total number have been superimposed, this indicates the station was sampled during both day and night. A black and white symbol indicates the same value was obtained for both day and night samples. Fine fraction is 330μm-180μm, medium fraction is 1000μm-330μm, and coarse fraction is >1000μm. For day and night samples representing size fractionation (b), the day sample (D) is shown on the station location and the night sample (N) either above or below.

fraction which predominated (i.e. >50%) at 17 of the 22 stations sampled (Figure 4.15b). Excluding the day sample at station FL12, where the coarse/medium and fine fractions were in equal proportions, the fine fraction was greater at all stations except those in Loch Fyne and surrounding the Island of Arran.

Corresponding measures of biomass were variable (Figure 4.16a) ranging from 0.20 (station C6) to 54.3ml m^{-3} (station AB30). These values were generally higher than those in March (Figure 4.12a) but the high levels of biomass observed at 10m (Figure 4.14a) were not attained. Biomass was relatively low in the Firth of Lorn, slightly higher on the Malin Shelf, and variable in the North Channel. Within the Firth of Clyde biomass tended to be low at stations in the outer region, on, or seaward of, the Great Plateau, and higher in the vicinity of the Island of Arran. Biomass was not, however, exceptionally high in Loch Fyne as was observed at 10m (Figure 4.14a).

Biomass partitioning among the three size fractions was variable throughout the study area (Figure 4.16b), particularly in the Firth of Lorn and North Channel. At station FL1 on the Malin Shelf, small-sized zooplankters still predominated, accounting for 93% of the fauna. However, at many stations the larger size-fractions made a substantial contribution to the overall biomass; >50% at 11 of 21 (52%) stations sampled. This was most prominent at stations in the inner Firth of Clyde, although at a number of stations throughout the study area the same trend was observed. Again, it should be noted that no data are provided for stations AB8 and AB38 where problems in fractionating the sample occurred at the time of collection.

4.2.1.4.1 Comparison of Day and Night Collections

Day and night collections from 30m were also examined to compare zooplankton numbers and biomass for station FL12 and Y3 (see Figure

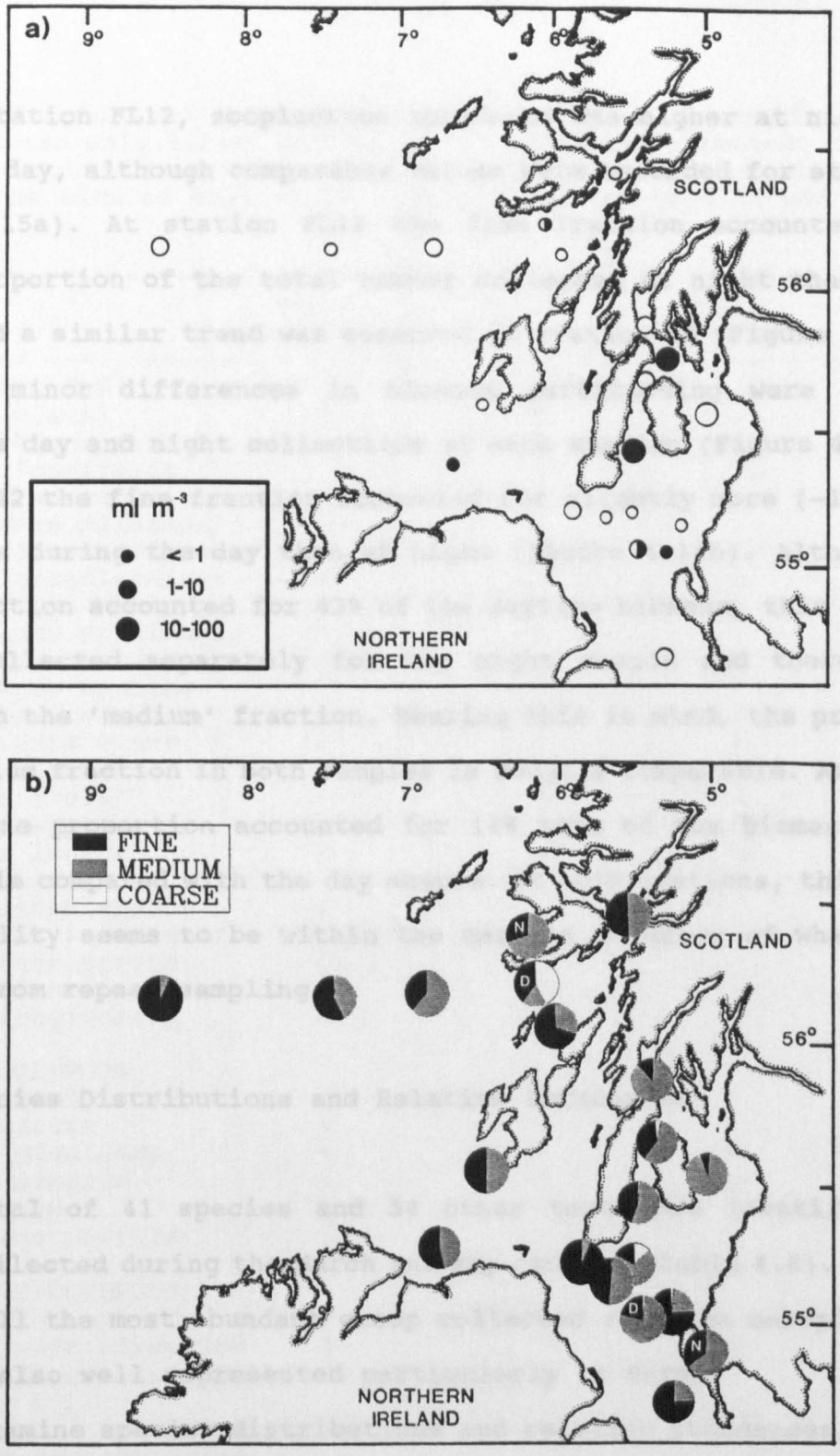


Figure 4.16 Total biomass of zooplankton collected at 30m in May 1986 (a), and the proportion in each size fraction (b). Empty circles represent stations sampled during day, solid circles represent stations sampled at night. Where values for total number have been superimposed, this indicates the station was sampled during both day and night. A black and white symbol indicates the same value was obtained for both day and night samples. Fine fraction is 330μm-180μm, medium fraction is 1000μm-330μm, and coarse fraction is >1000μm. For day and night samples representing size fractionation (b), the day sample (D) is shown on the station location and the night sample (N) either above or below.

3.1). At station FL12, zooplankton abundance was higher at night than during the day, although comparable values were recorded for station Y3 (Figure 4.15a). At station FL12 the fine fraction accounted for a greater proportion of the total number collected at night than during the day and a similar trend was observed at station Y3 (Figure 4.15b).

Only minor differences in biomass partitioning were observed between the day and night collections at each station (Figure 4.16). At station FL12 the fine fraction accounted for slightly more (~13.5%) of the biomass during the day than at night (Figure 4.16b). Although the coarse fraction accounted for 43% of the daytime biomass, this fraction was not collected separately for the night sample and therefore is included in the 'medium' fraction. Bearing this in mind, the proportion of the medium fraction in both samples is roughly comparable. At station Y3, the fine proportion accounted for 14% more of the biomass in the night sample compared with the day smaple. At both stations, this degree of variability seems to be within the margins of error of what may be expected from repeat sampling.

4.2.2 Species Distributions and Relative Abundances

A total of 41 species and 34 other taxa were identified from samples collected during the March and May cruises (Table 4.6). Copepods were overall the most abundant group collected although meroplanktonic taxa were also well represented particularly in March.

To examine species distributions and relative abundances, species or other taxa which comprised at least 3% of the total number at one or more stations were selected and designated as being 'common'. Their distributions and relative abundances, with the exception of 'unidentified eggs' and 'appendicularians', are shown in Figures 4.17 to 4.20 for samples collected at 10m and 30m during the March and May cruises. Since many species and taxa were common members of the fauna

Table 4.6 Zooplankton collected at 10m and 30m in March 1987 and May 1986. * denotes only larval and/or juvenile stages collected. C denotes that a species or taxon was common (accounting for ≥ 3% of the overall fauna) at the time of collection, while + denotes that it was not.

GROUP Species	March 10m	March 30m	May 10m	May 30m
CALANOID COPEPODS				
Acartia clausi	C	C	C	C
Acartia discaudata			+	+
Acartia longiremis		+		
Aetideus armatus		+	+	
Anomalocera patersoni	+		+	+
Calanus finmarchicus	+	C	C	C
Calanus helgolandicus	+	+	+	+
Calanus spp.	C	C	C	C
Calocalanus styliremis	+	+		
Centropages hamatus	C	+	C	C
Centropages typicus			+	+
Clausocalanus spp.		+	+	+
Ctenocalanus vanus		+	+	+
Diaixis hibernica	+			
Euchaeta acuta		+	+	
Isias clavipes			+	+
Metridia lucens	+	+	+	+
Metridia longa				+
Microcalanus spp.	C	C	C	C
Neocalanus tenuicornis				+
Paracalanus parvus	C	C	+	C
Pseudocalanus spp.	C	C	C	C
Temora longicornis	C	C	C	C
CYCLOPOID COPEPODS				
Corycaeus anglicus		+		+
Oncaea minuta	+			
Oithona plumifera	+	+		+
Oithona similis	+	C	+	+
Oithona spp.	C	C	C	C
Paroithona parvula		+		
HARPACTICOID COPEPODS				
**Longipedia* spp.	+			+
Microsetella norvegica	+	+	+	
Unidentified harpacticoid	+	+		
AMPHIPODS				
Parathemisto abyssorum		+		+
Parathemisto gracilipes	+			
Benthic amphipod		+		
Hyperiid amphipod		+		
CHAETOGNATHS				
Sagitta elegans	+	+	+	+
Sagitta tasmanica			+	
Sagitta spp.		+	+	+

Table 4.6 Concluded.

GROUP Species	March 10m	March 30m	May 10m	May 30m
CLADOCERANS				
Evadne nordmanni	+	+	C	C
Podon intermedius		+		
Podon leuckartii	+	+	C	C
EUPHAUSIIDS				
**Meganyctiphanes norvegica*		+	+	+
**Thysanoessa longicaudata*	+	+		+
**Thysanoessa raschii*	C	C	+	+
Thysanoessa spp.		+	+	+
BRYOZOANS				
**Electra pilosa*	C	C	C	C
**Membranipora membranacea*	+	+	+	+
DECAPODS				
**Nephrops norvegicus*				+
**Sergestes* spp.				+
Brachyuran zoeae	C	+	C	C
Caridean zoeae	+	+	+	+
Galatheid zoeae		+	+	+
Pagurid zoeae	+	+	+	+
GELATINOUS ZOOPLANKTON				
Aglantha digitale				+
Appendicularians	C	C	C	C
Medusae		+	C	+
Siphonophora				+
MISCELLANEOUS HOLOPLANKTON				
Copepod nauplii	C	C	C	C
Euphausiid eggs	C	C	+	+
Euphausiid nauplii	C	C		+
*Opisthobranchia	+	+	+	+
Ostracods	+			+
Pycnogonids				+
Tomopteris helgolandica			+	+
Unidentified copepodids	C	C	C	C
Unidentified eggs	C	C	C	C
MISCELLANEOUS MEROPLANKTON				
*Anenome				+
Ascidian		+		
Bivalve larvae	+	+	+	+
Cirripede nauplii	C	C	C	C
Cyprid	+	+	C	C
*Echinoderms	+	+	+	
Gastropod larvae	+	+	+	+
**Littorina littorea*	C	C	+	+
Polychaete larvae	C	C	+	+
*Prosobranchia	+	+	+	+

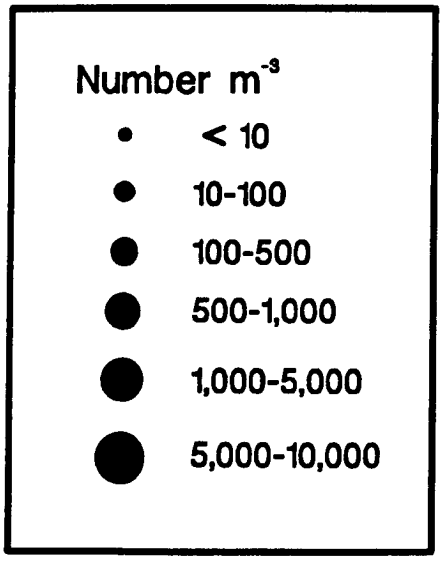
at all times, a similar order of presentation was used in all figures, as much as possible. As with total zooplankton numbers and biomass, large scale increments were used in the preparation of these figures in an attempt to minimize the effects of day/night sampling and species patchiness. For clarity, only the scale increments used in each figure are shown in the corresponding legend; the full scale range is given in the preceding figure captions. For the May cruise (Figures 4.19 and 4.20) mean values of abundance, calculated using day and night samples combined, are shown for species and taxa at stations FL12 and Y3.

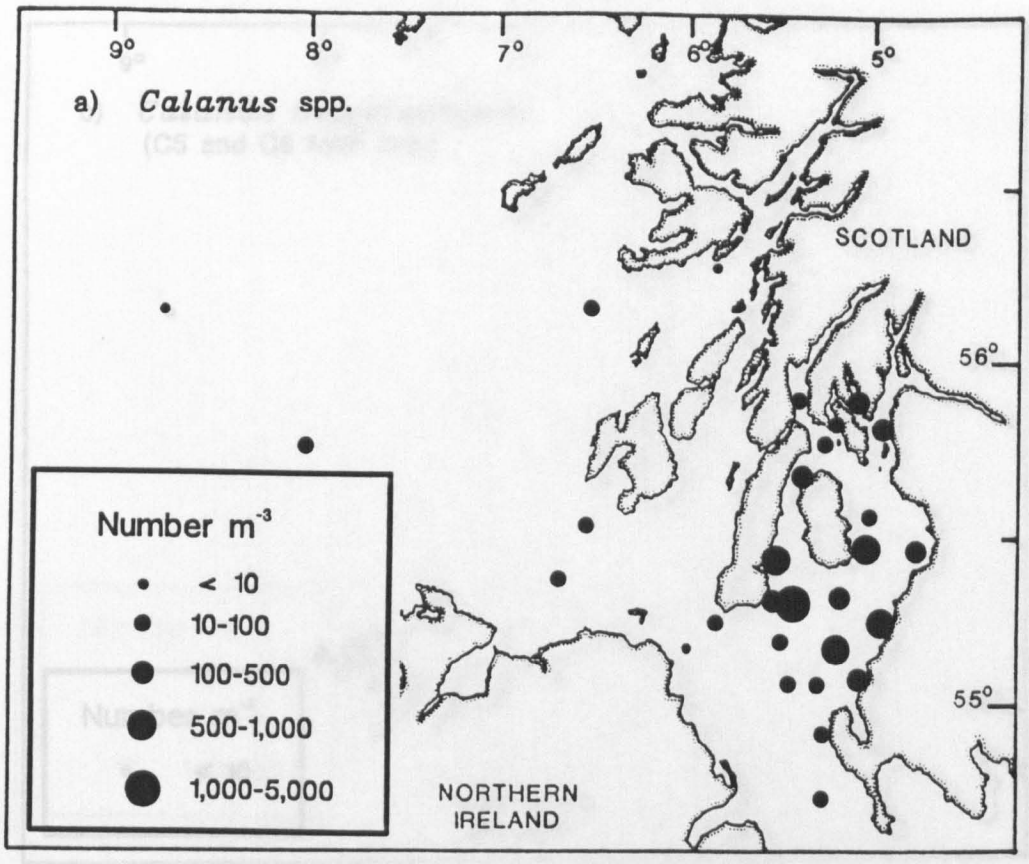
4.2.2.1 March 1987: 10m

A total of 22 species and 25 other taxa was identified from samples collected at 10m during the March cruise (Table 4.6). Of these, 20 were common, and their distributions and relative abundances are shown in Figure 4.17. *Calanus finmarchicus* and *C. helgolandicus* did not meet the criterion for selection because only stages C5 and C6 were routinely identified. However, their distribution throughout the study area is shown in Figures 4.17b and 4.17c for comparison with that of *Calanus* spp. (Figure 4.17a) which represents the earlier copepodid stages, C1 to C4, of these species.

At least eight species of copepods were common members of the fauna at 10m, many of which were ubiquitous in distribution, e.g., *Pseudocalanus* spp. (Figure 4.17d), *Acartia clausi* (Figure 4.17e), *Microcalanus* spp. (Figure 4.17f), and *Oithona* spp. (Figure 4.17g). Others, although widespread, were absent from particular geographical regions: *Temora longicornis* (O.F. Müller) (Figure 4.17h) occurred in all regions with the exception of the Malin Shelf, *Paracalanus parvus* (Figure 4.17i) was concentrated primarily offshore, and *Centropages hamatus* (Figure 4.17j) was distributed mainly throughout the Firth of Clyde. These species all occurred in relatively low abundances, *T.*

Figure 4.17 Distribution of 'common' species collected at stations sampled at 10m in March 1987. The full range of values used in this figure is shown below.





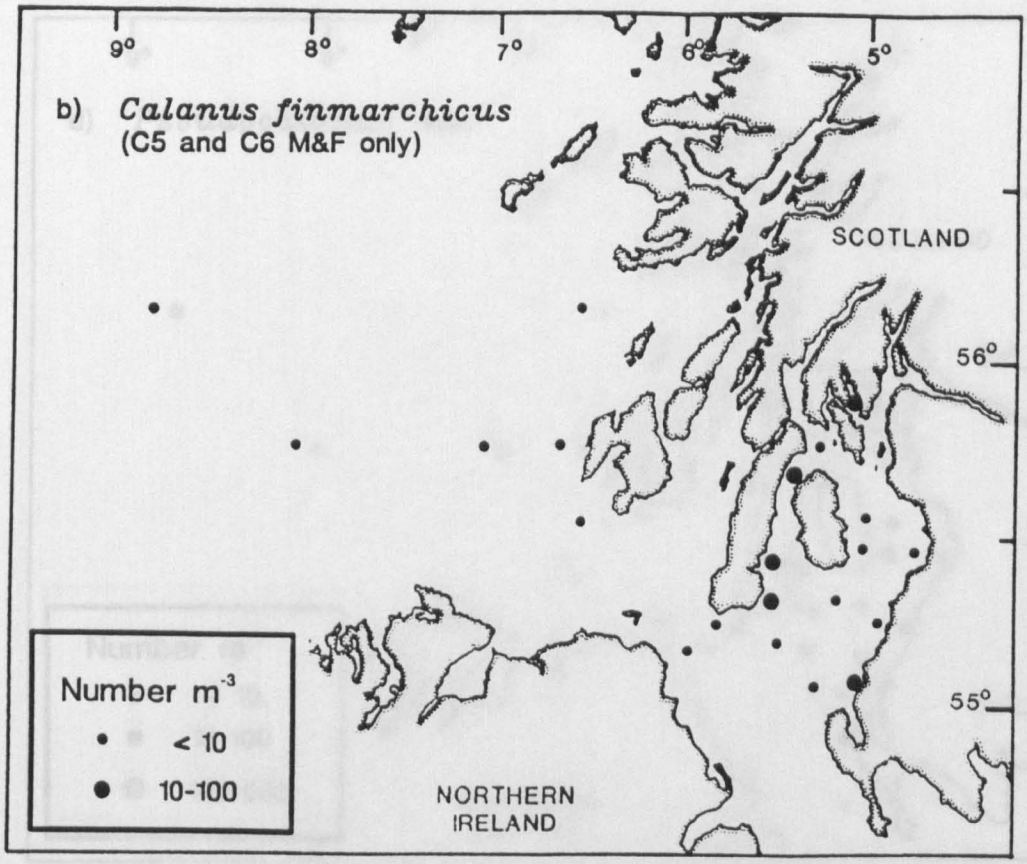
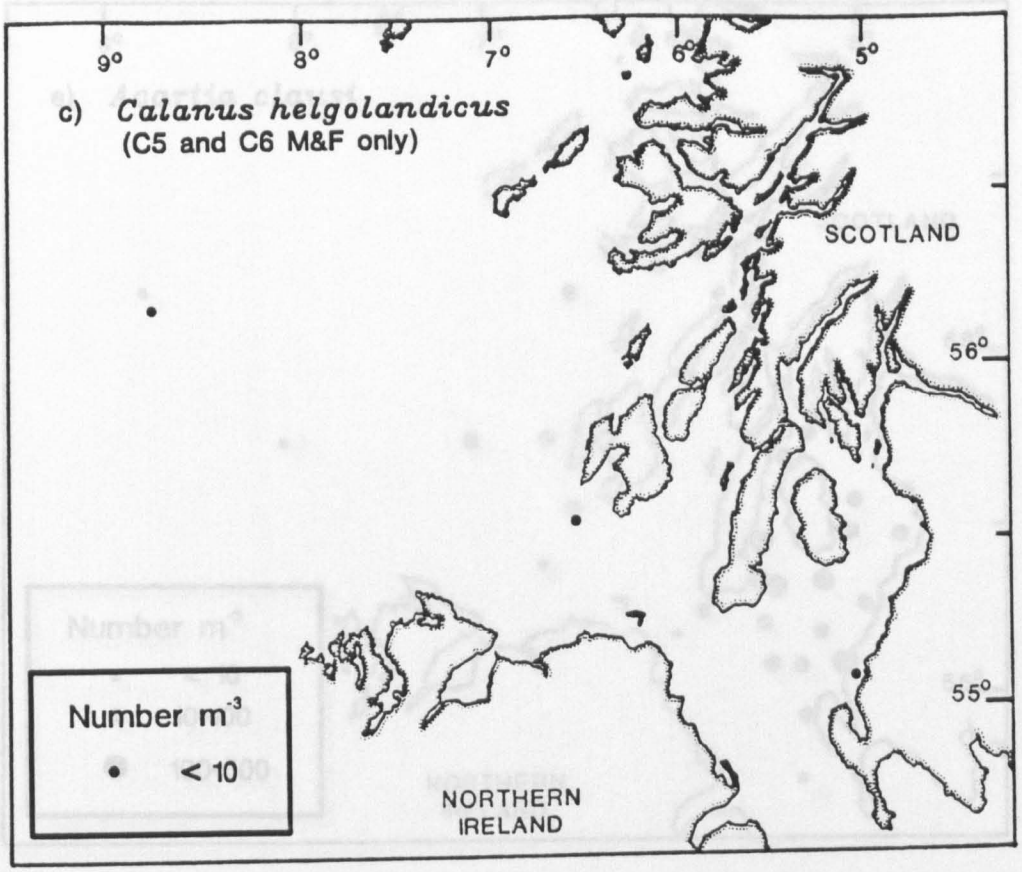


Figure 4.17 (Continued). Distribution of *Calanus* spp. (a) and *Calanus finmarchicus*, stages C5 and C6 only, (b) collected at 10m in March 1987.



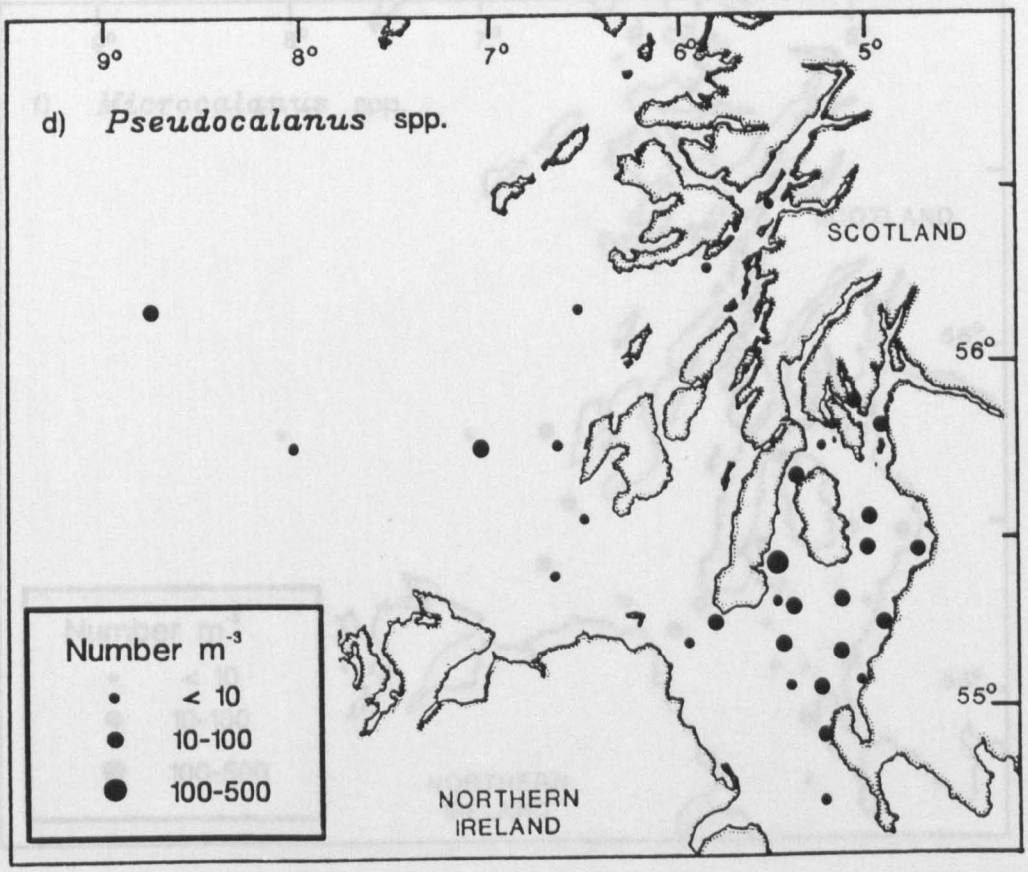
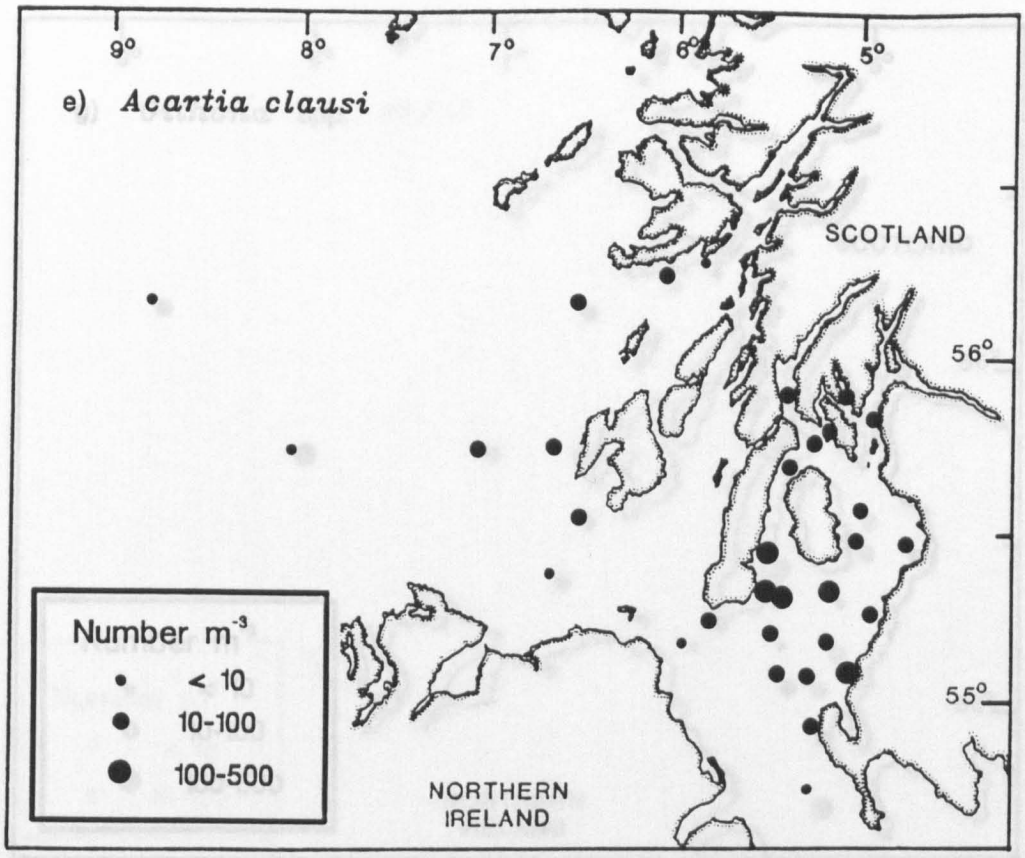


Figure 4.17 (Continued). Distribution of *Calanus helgolandicus*, stages C5 and C6 only, (c) and *Pseudocalanus* spp. (d) collected at 10m in March 1987.



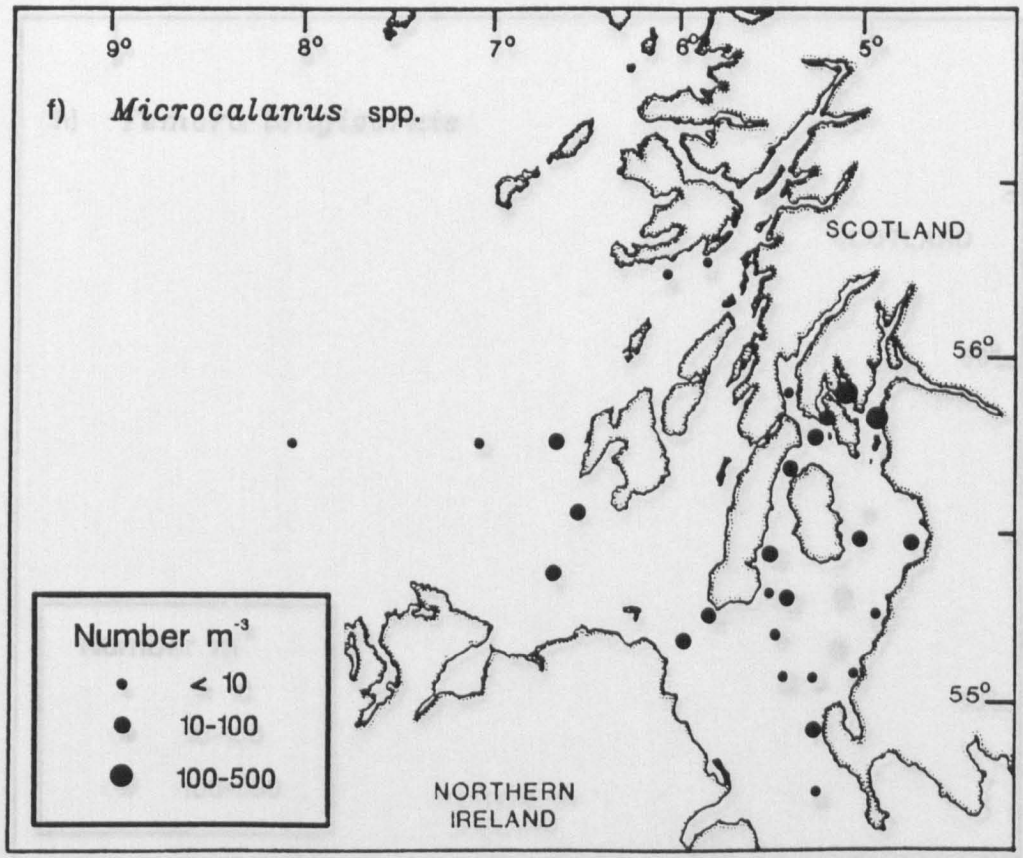
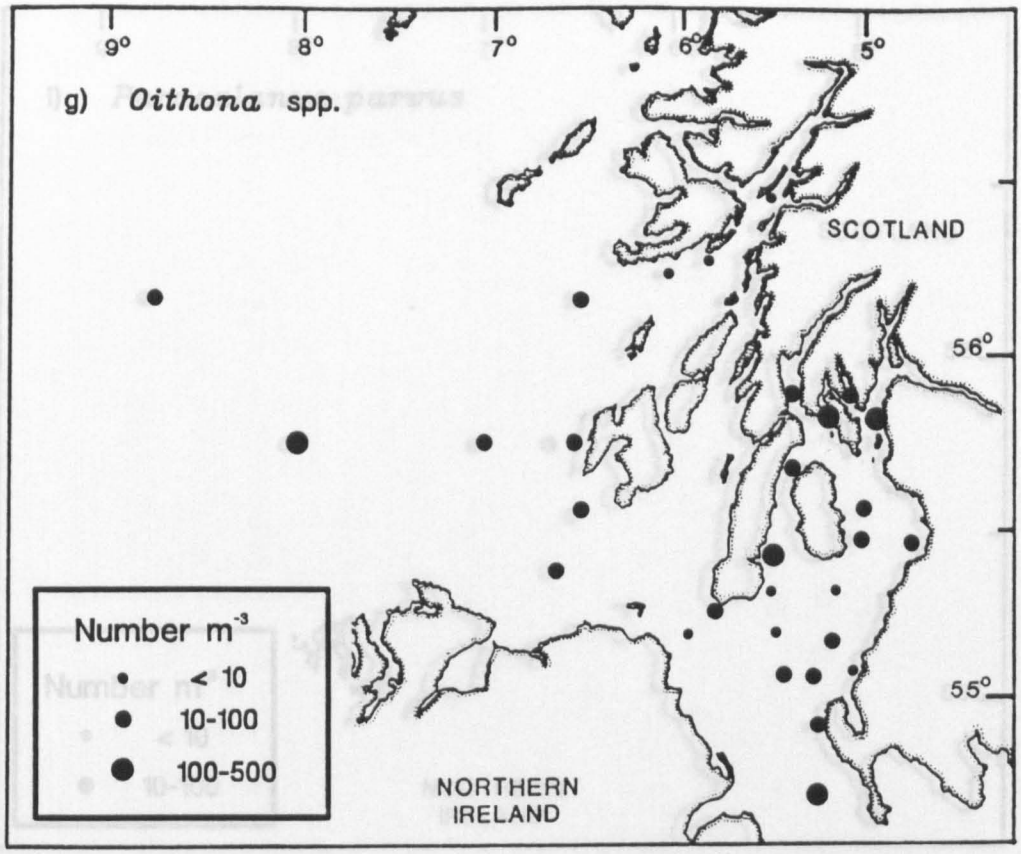


Figure 4.17 (Continued). Distribution of *Acartia clausi* (e) and *Microcalanus* spp. (f) collected at 10m in March 1987.



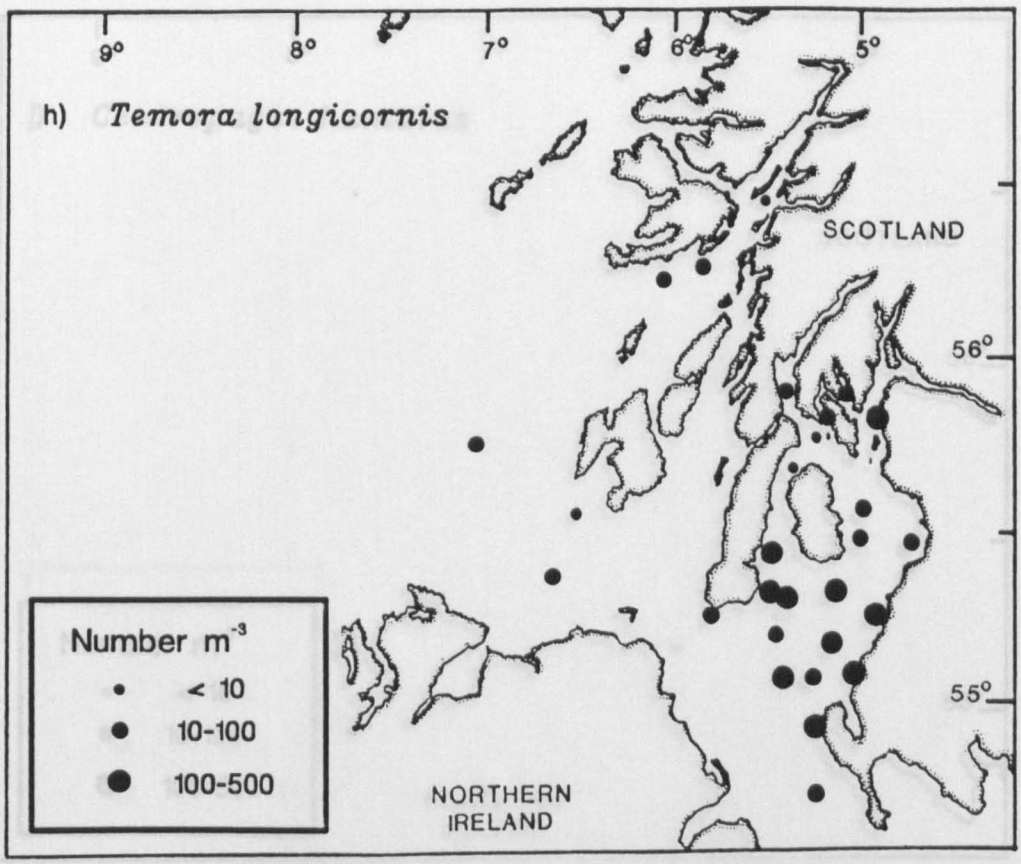
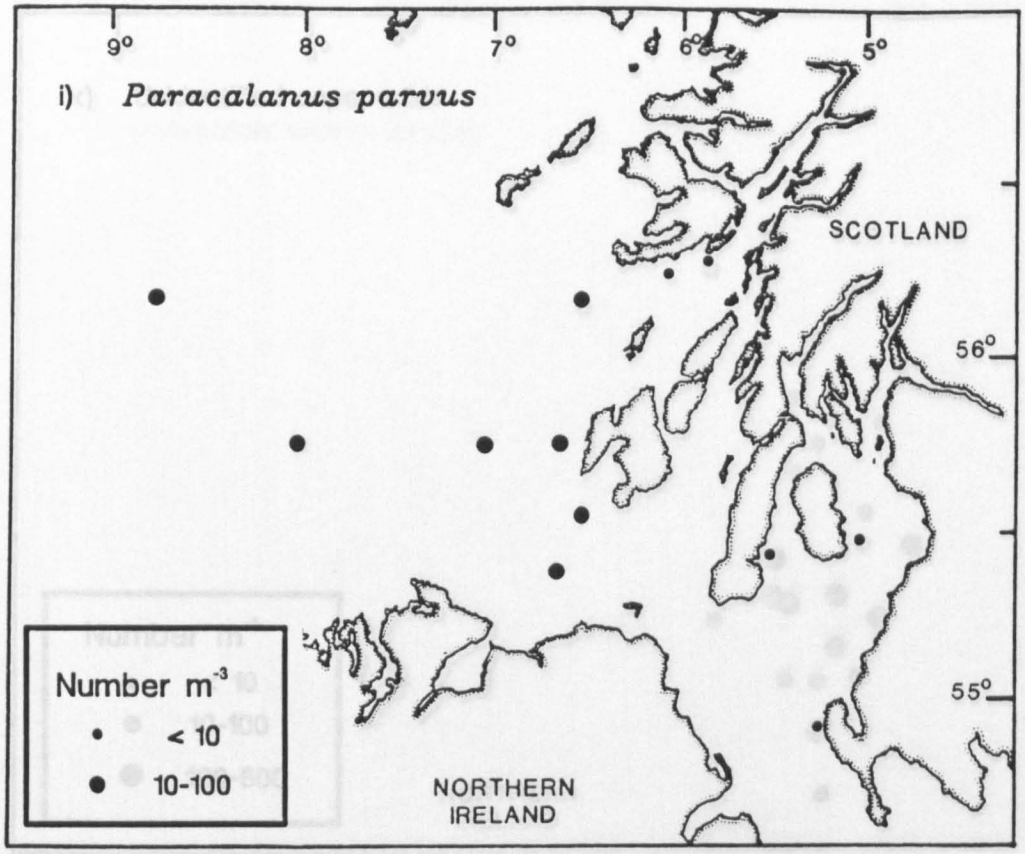


Figure 4.17 (Continued). Distribution of *Oithona* spp. (g) and *Temora longicornis* (h) collected at 10m in March 1987.



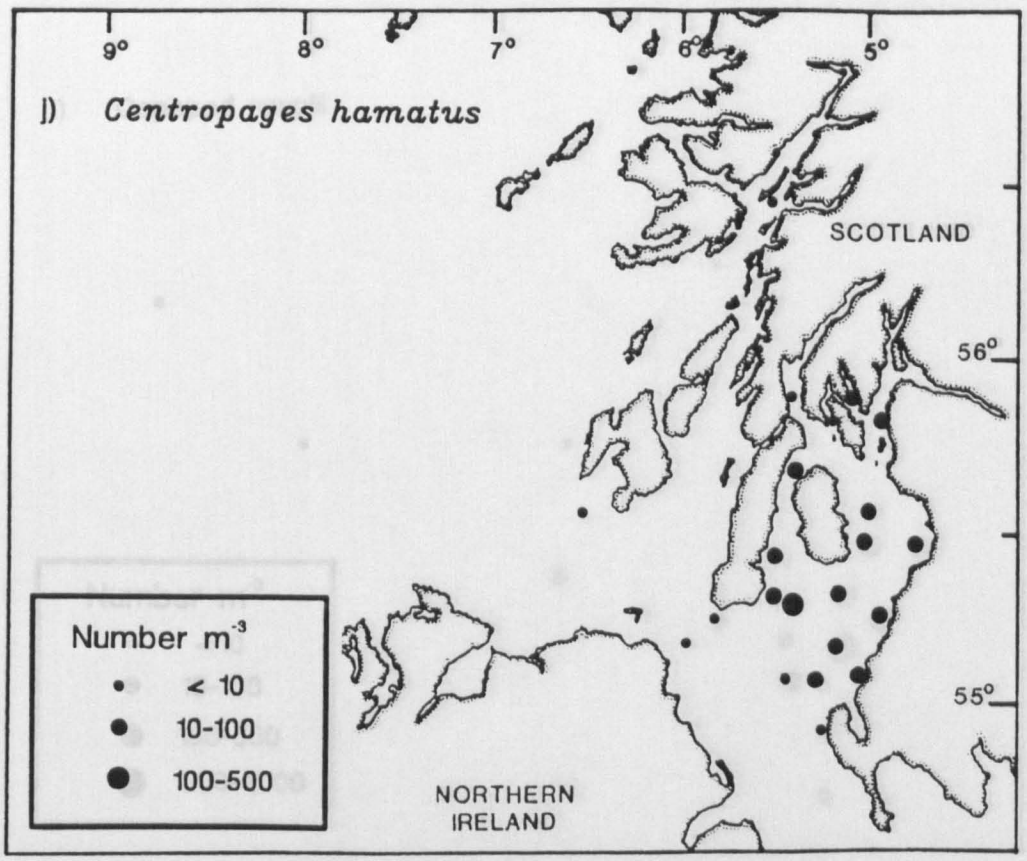
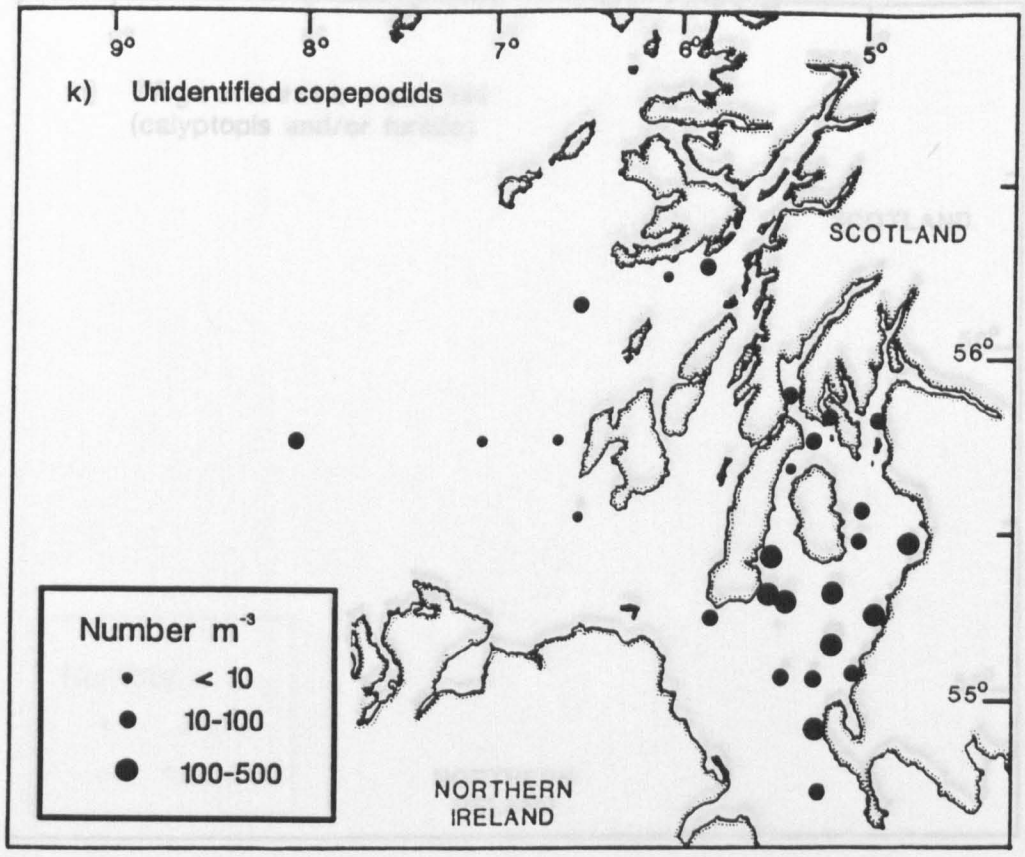


Figure 4.17 (Continued). Distribution of *Paracalanus parvus* (i) and *Centropages hamatus* (j) collected at 10m in March 1987.



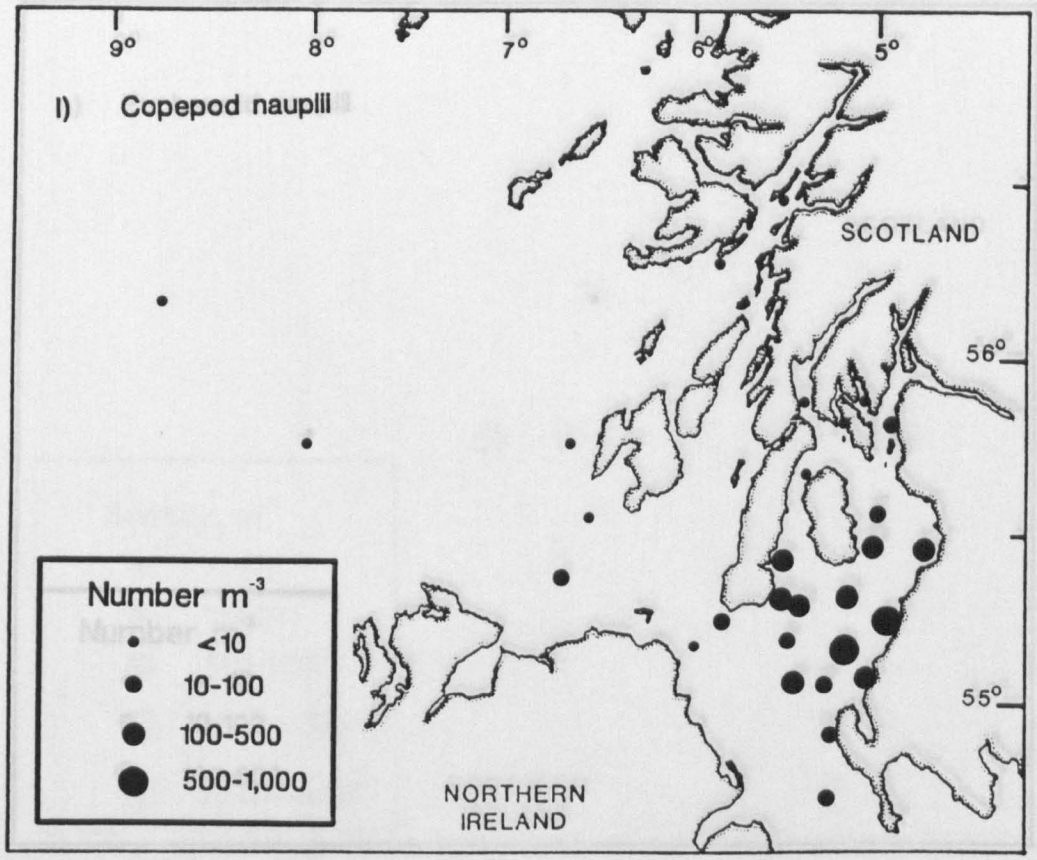
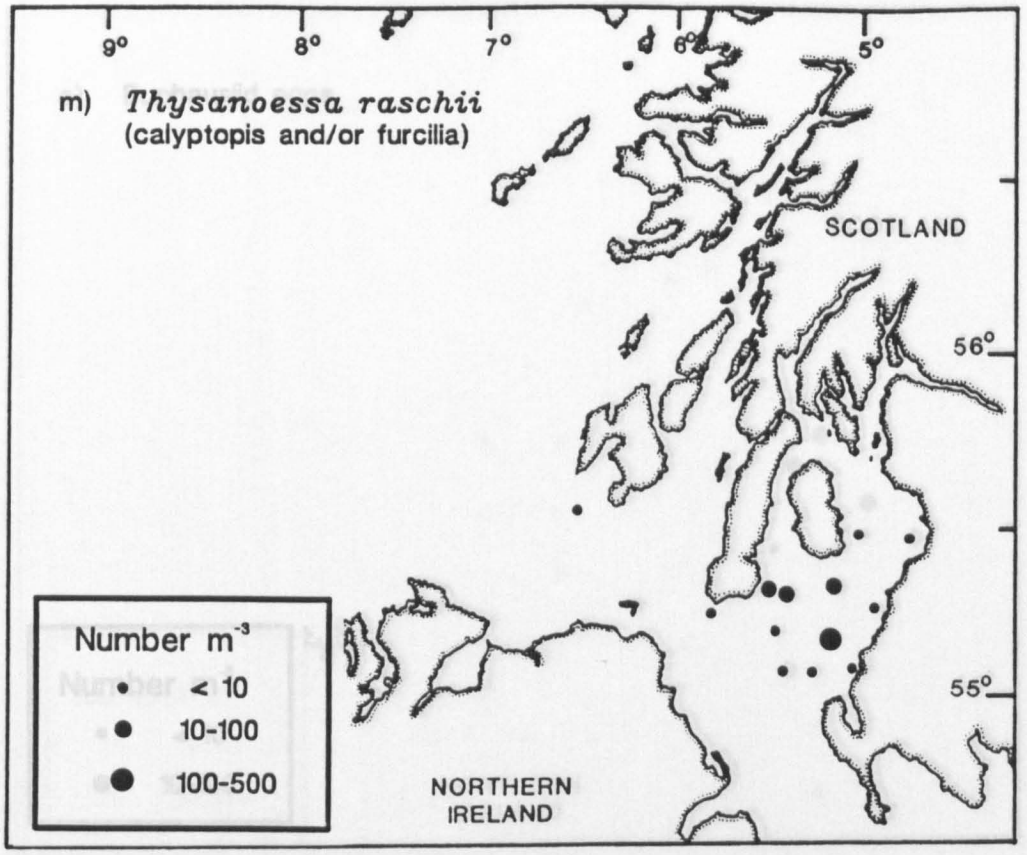


Figure 4.17 (Continued). Distribution of unidentified copepodids (k) and copepod nauplii (l) collected at 10m in March 1987.



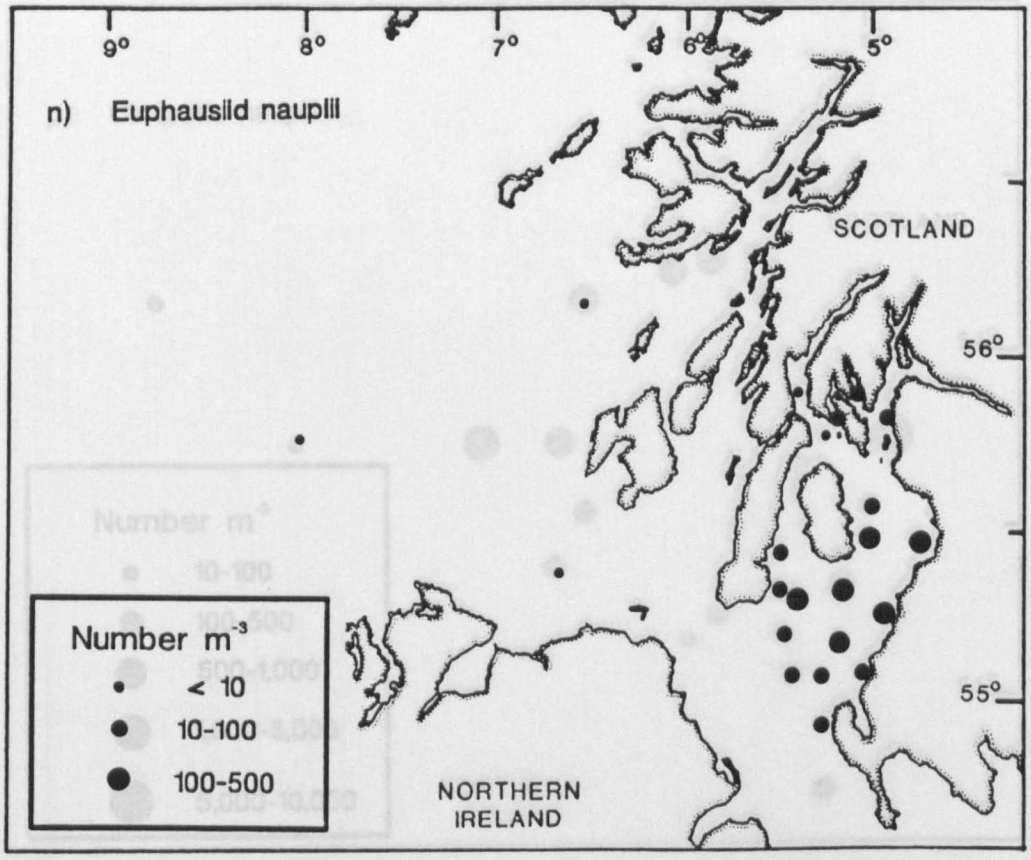
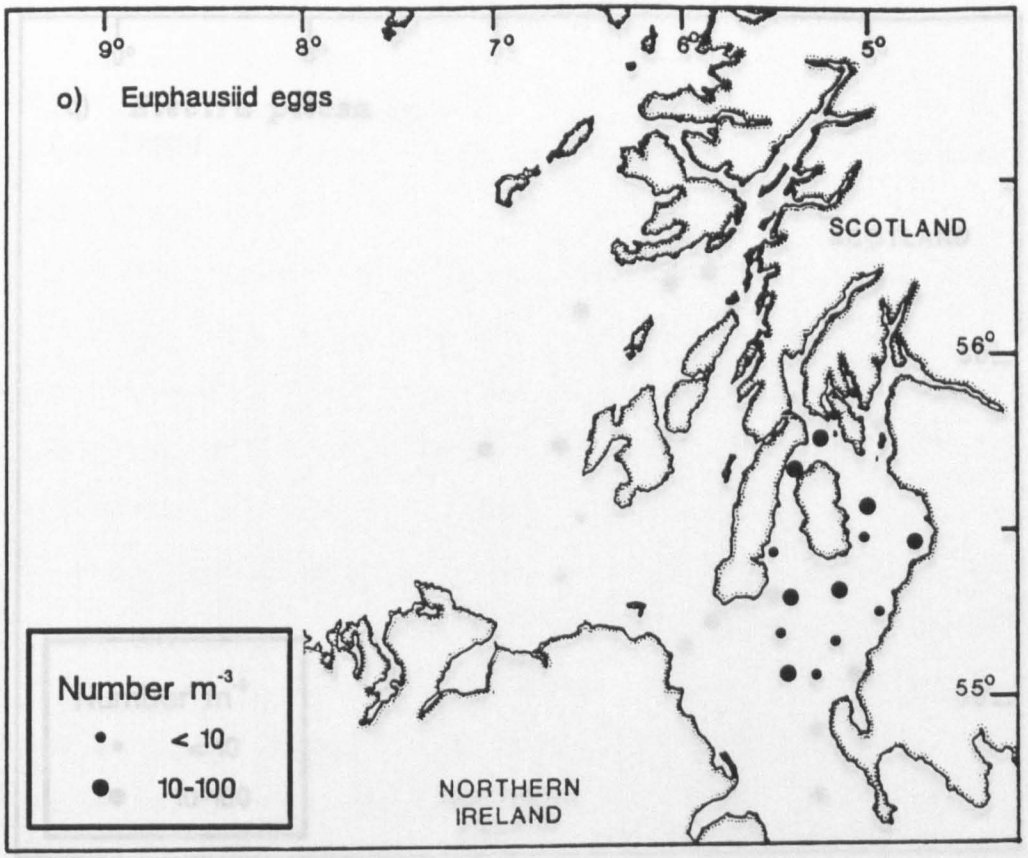


Figure 4.17 (Continued). Distribution of *Thysanoessa raschii*, calyptopis and/or furcilia, (m) and euphausiid nauplii (n) collected at 10m in March 1987.



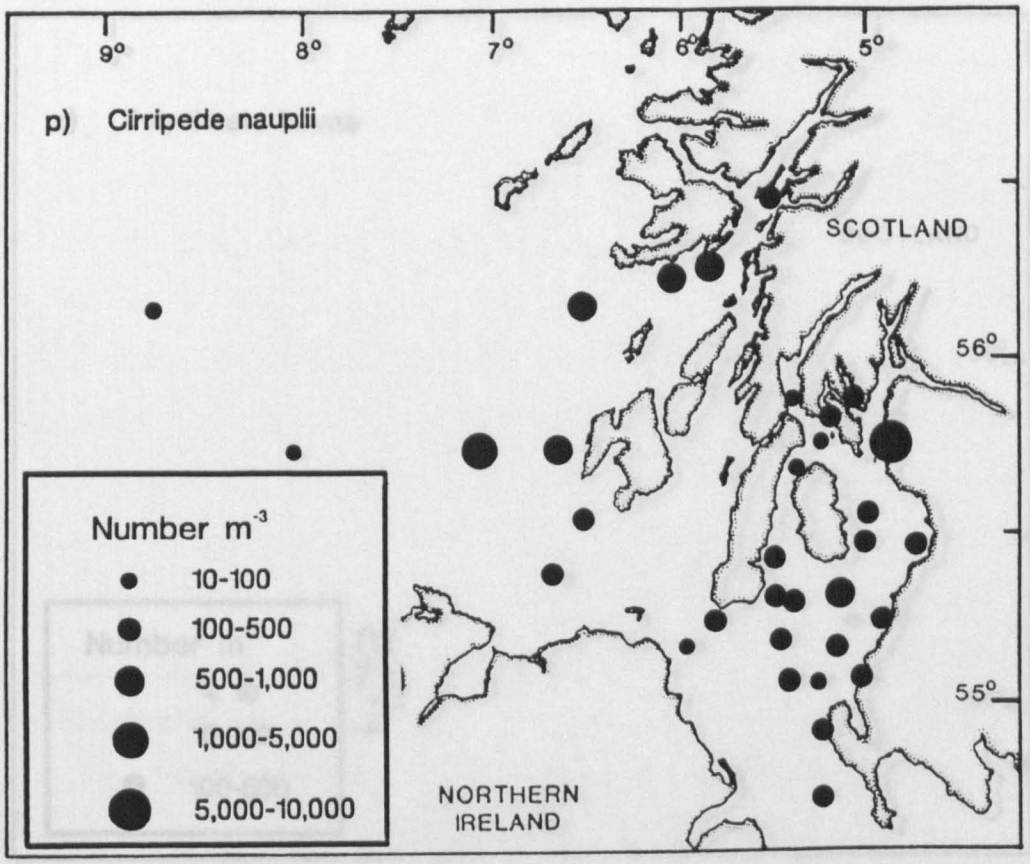
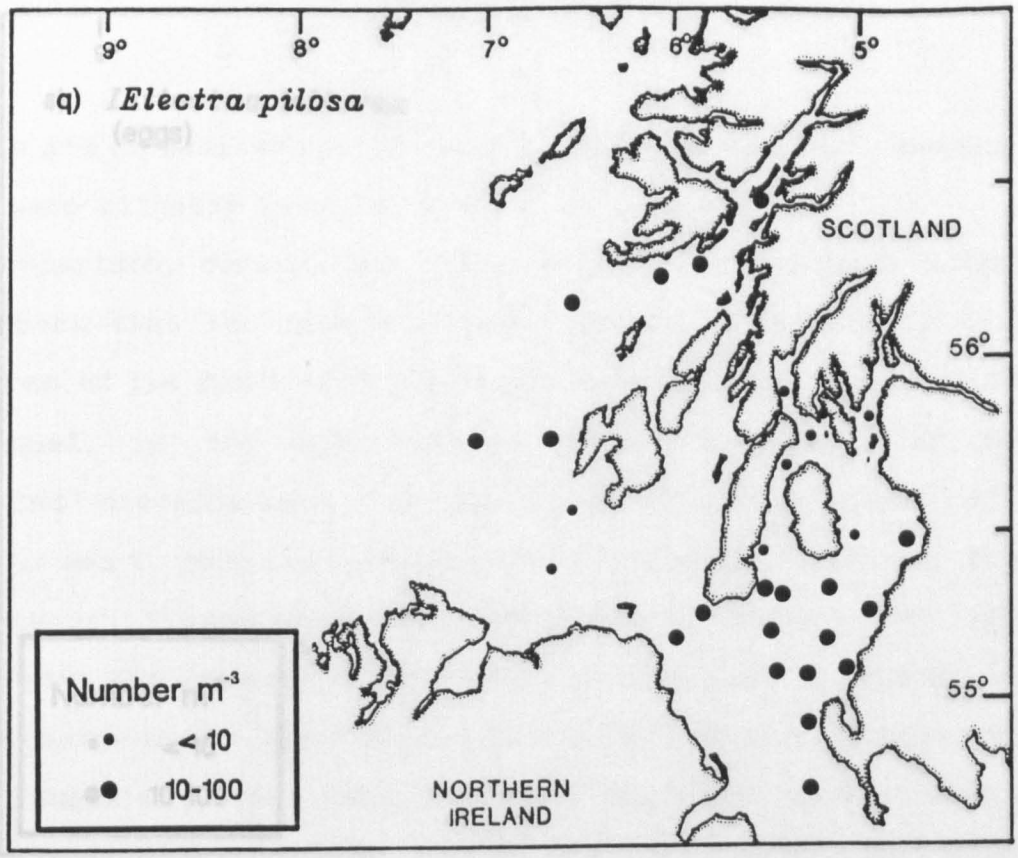


Figure 4.17 (Continued). Distribution of euphausiid eggs (o) and cirripede nauplii (p) collected at 10m in March 1987.



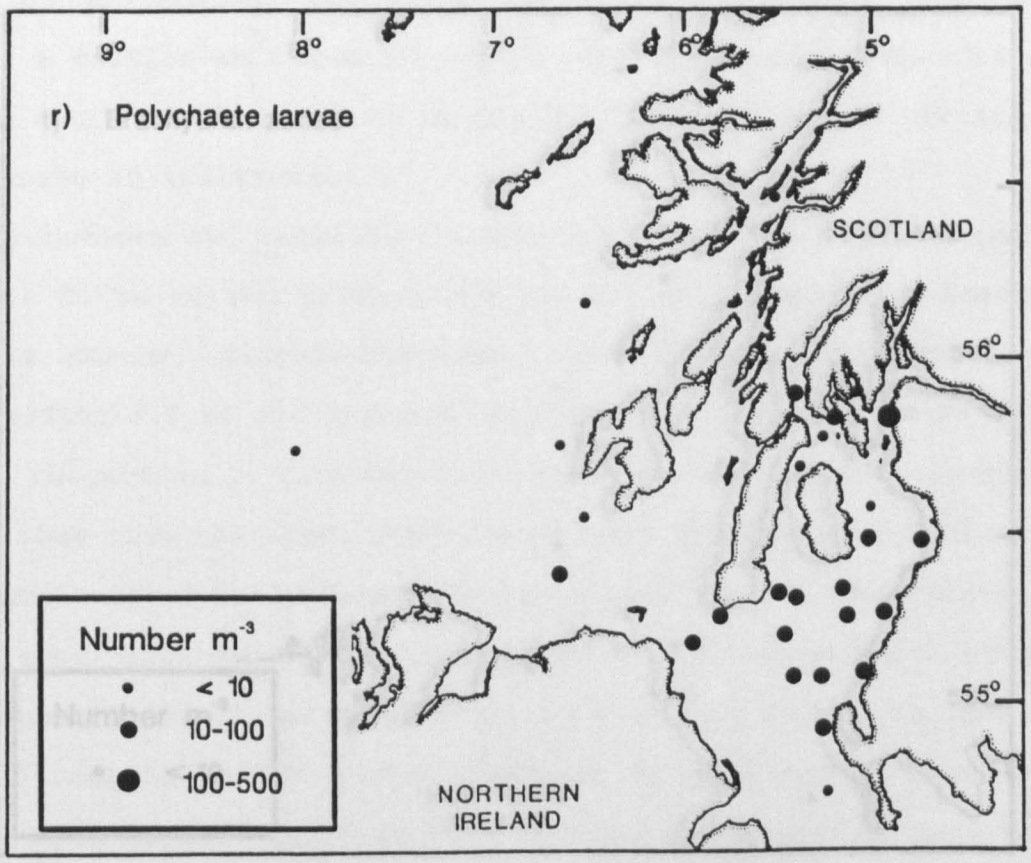
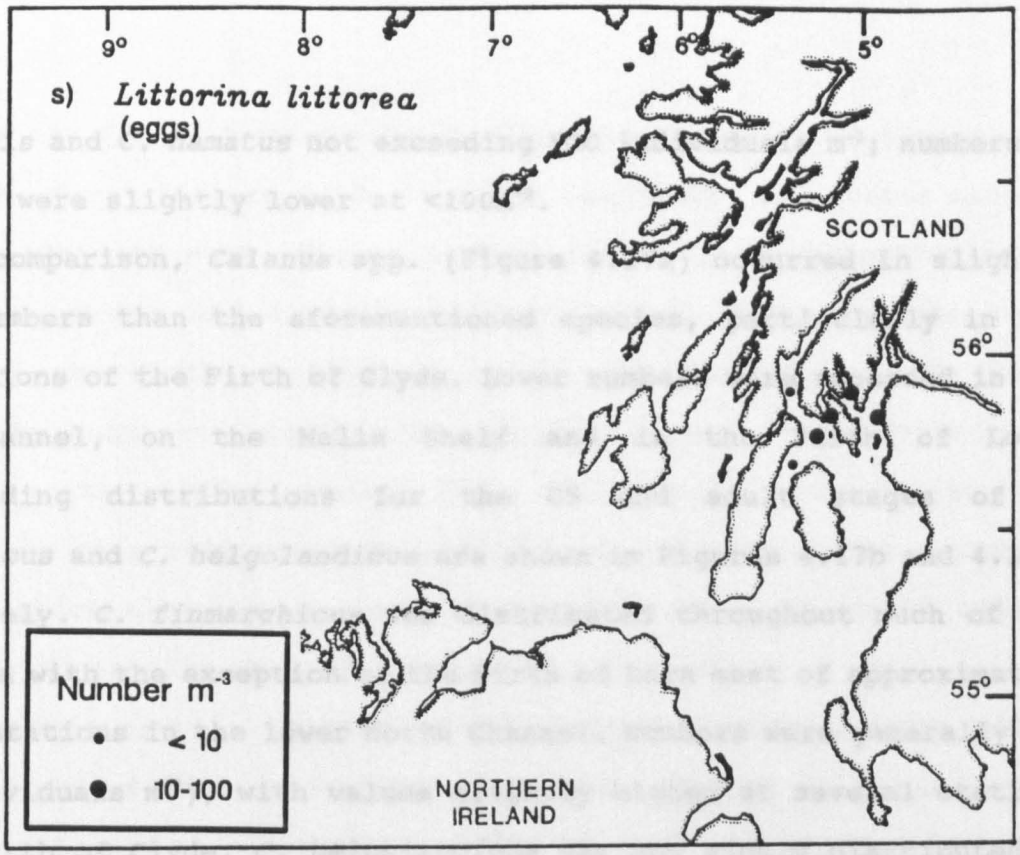


Figure 4.17 (Continued). Distribution of *Electra pilosa* (q) and polychaete larvae (r) collected at 10m in March 1987.



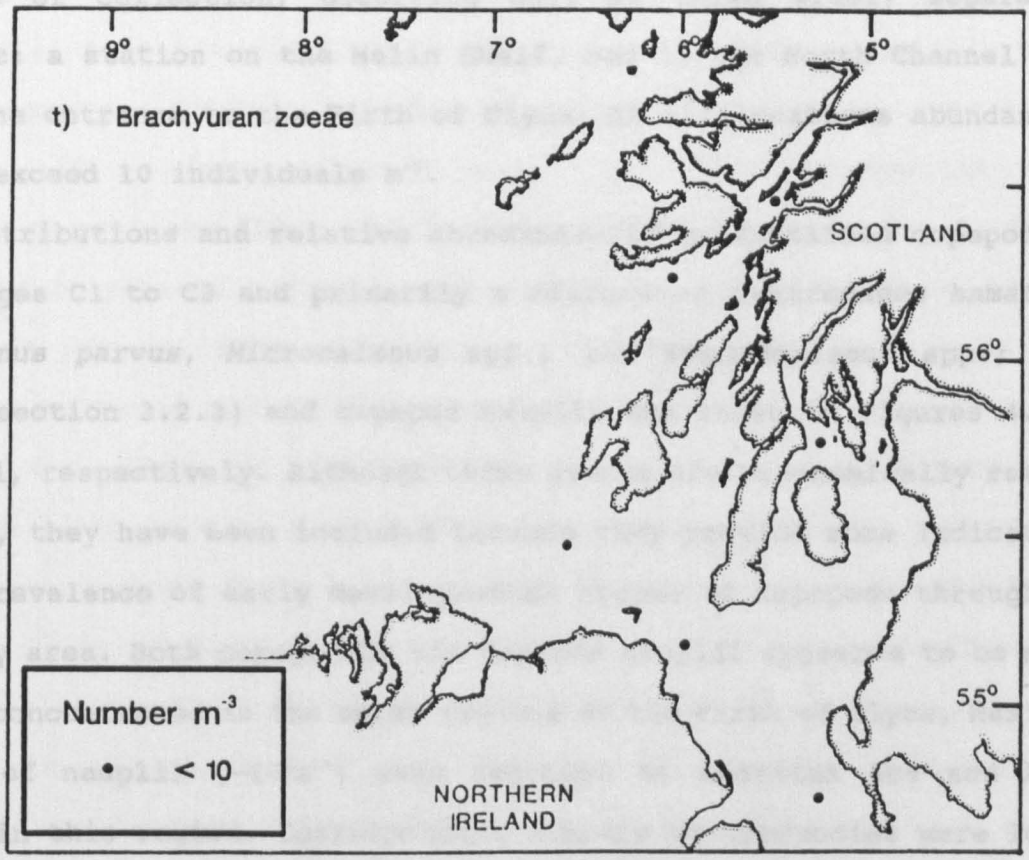


Figure 4.17 (Continued). Distribution of *Littorina littorea*, eggs only, (s) and Brachyuran zoeae (t) collected at 10m in March 1987.

longicornis and *C. hamatus* not exceeding 500 individuals m^{-3}; numbers of *P. parvus* were slightly lower at $<100m^{-3}$.

By comparison, *Calanus* spp. (Figure 4.17a) occurred in slightly higher numbers than the aforementioned species, particularly in the outer regions of the Firth of Clyde. Lower numbers were recorded in the North Channel, on the Malin Shelf and in the Firth of Lorn. Corresponding distributions for the C5 and adult stages of *C. finmarchicus* and *C. helgolandicus* are shown in Figures 4.17b and 4.17c, respectively. *C. finmarchicus* was distributed throughout much of the study area with the exception of the Firth of Lorn east of approximately 6°W, and stations in the lower North Channel. Numbers were generally low (<10 individuals m^{-3}), with values slightly higher at several stations in the Firth of Clyde. *C. helgolandicus* was not widely distributed at the time of collection, occurring only at three widely separated locations: a station on the Malin Shelf, one in the North Channel and one at the entrance to the Firth of Clyde. At all locations abundances did not exceed 10 individuals m^{-3}.

Distributions and relative abundances of unidentified copepodids (i.e stages C1 to C3 and primarily a mixture of *Centropages hamatus*, *Paracalanus parvus*, *Microcalanus* spp., and *Pseudocalanus* spp.; see Methods section 3.2.3) and copepod nauplii are shown in Figures 4.17k and 4.17l, respectively. Although these groups are taxonomically rather nebulous, they have been included because they provide some indication of the prevalence of early developmental stages of copepods throughout the study area. Both copepodids and copepod nauplii appeared to be most heavily concentrated in the outer regions of the Firth of Clyde. Maximum numbers of nauplii ($\sim10^3m^{-3}$) were recorded at stations AB8 and AB22 located in this region. Corresponding numbers of copepodids were lower (generally $<500m^{-3}$). Copepodids and nauplii also occurred throughout much of the remaining study region in low numbers.

In addition to copepods, eight other species or taxa were common

members of the fauna at 10m in March. With the exception of *Thysanoessa raschii* (M. Sars) (Figure 4.17m) and the associated euphausiid nauplii (Figure 4.17n) and eggs (Figure 4.17o), most were meroplanktonic. *T. raschii* calyptopis and furcilia were collected only from the outer regions of the Firth of Clyde and from two stations in the North Channel. In contrast, euphausiid nauplii and eggs were distributed throughout the Clyde. Their more widespread distribution was attributable to a mixture of *T. raschii* and *Meganyctiphanes norvegica* (M. Sars) which also occurred in the region (Table 4.6). Small numbers of euphausiid nauplii were also observed offshore.

Cirripede nauplii (Figure 4.17p), cyphonautes of *Electra pilosa* (Linné) (Figure 4.17q), and polychaete larvae (Figure 4.17r) were also widely distributed throughout most of the study area. Numbers of nauplii were consistently high in the Firth of Lorn relative to other taxa collected at this time. Elsewhere, abundance was highly variable with maximum numbers (~8000m^{-3}) recorded at station AB34 in the inner Firth of Clyde. It is interesting to note that cirripede nauplii were collected at stations FL0 and D0 in the region of the Malin Shelf. Small numbers of polychaete larvae were also collected at station D0 but *E. pilosa* was not collected west of approximately 7°W. These last two species occurred in comparable numbers, generally <100m^{-3}.

The two remaining meroplanktonic taxa, eggs of the gastropod *Littorina littorea* and brachyuran zoeae, occurred in low numbers in limited areas. Eggs of *L. littorea* were collected only from the inner Firth of Clyde (Figure 4.17s) while brachyuran zoeae (thought to be mostly *Portunus puber*) were collected primarily from stations in the inner Firth of Lorn and North Channel (Figure 4.17t). Numbers of brachyuran zoeae were consistently low at <10m^{-3}, while those of *L. littorea* eggs were slightly higher but not exceeding 100m^{-3}.

4.2.2.2 March 1987: 30m

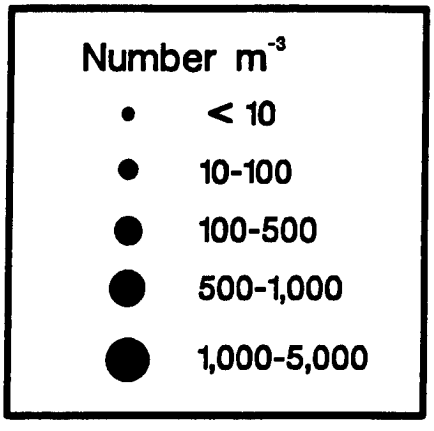
At 30m, a total of 28 species and 30 other taxa was identified from the collected samples (Table 4.6). Twenty species or other taxa were designated 'common' and these were identical to those at 10m with the following exceptions: *Centropages hamatus* and brachyuran zoeae were common at 10m but not at 30m, while *Calanus finmarchicus* and *Oithona similis* (C6 males only) were common only at 30m. Distribution patterns of all common species are presented in Figure 4.18.

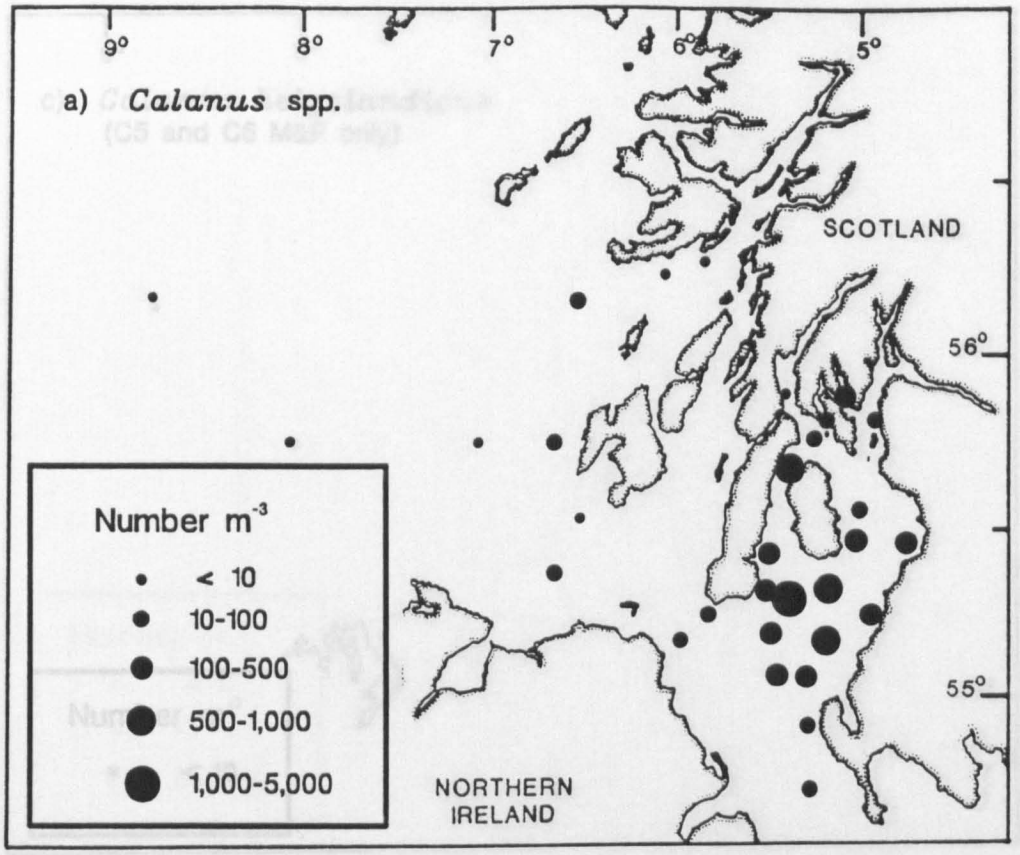
Copepods accounted for 9 of the 20 common species or other taxa at 30m. Distribution patterns for these species largely reflected those observed at 10m (Figure 4.17) although often with subtle differences in frequency of occurrence and/or relative abundances. In general, the four species, *Pseudocalanus* spp. (Figure 4.18d), *Acartia clausi* (Figure 4.18e), *Microcalanus* spp. (Figure 4.18f) and *Oithona* spp. (Figure 4.18g) were ubiquitous. Numbers of *Microcalanus* spp., *Oithona* spp., and *Pseudocalanus* spp. were $<500m^{-3}$, while *A. clausi* did not exceed $100m^{-3}$. *O. similis*, represented by adult males only, was also common at 30m (Figure 4.18h) and widely distributed with the exception of the Firth of Lorn and lower regions of the North Channel. Numbers collected were generally low throughout the study area at $<10m^{-3}$; slightly higher values were occasionally recorded in the Firth of Clyde and at station D7.

Distributions of *Temora longicornis* and *Paracalanus parvus* were similar to those at 10m; the former species was widely distributed apart from the Malin Shelf (Figure 4.18i), the latter concentrated primarily in the Firth of Lorn and on the Malin Shelf (Figure 4.18j). Numbers of *T. longicornis* were somewhat lower at 30m than at 10m at stations in the outer Firth of Clyde, while *P. parvus* was widely distributed in low numbers ($<10m^{-3}$) throughout the Clyde.

Once again *Calanus* spp. occurred in high numbers relative to other

Figure 4.18 Distribution of 'common' species collected at stations sampled at 30m in March 1987. The full range of values used in this figure is shown below.





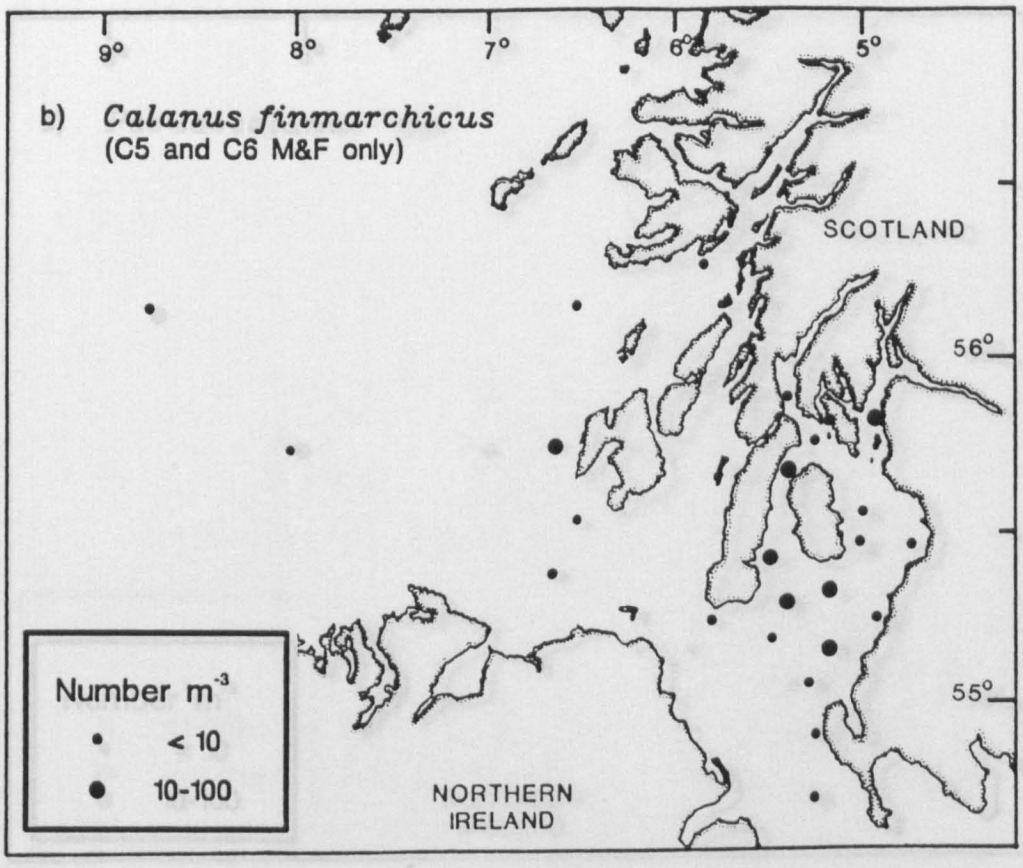
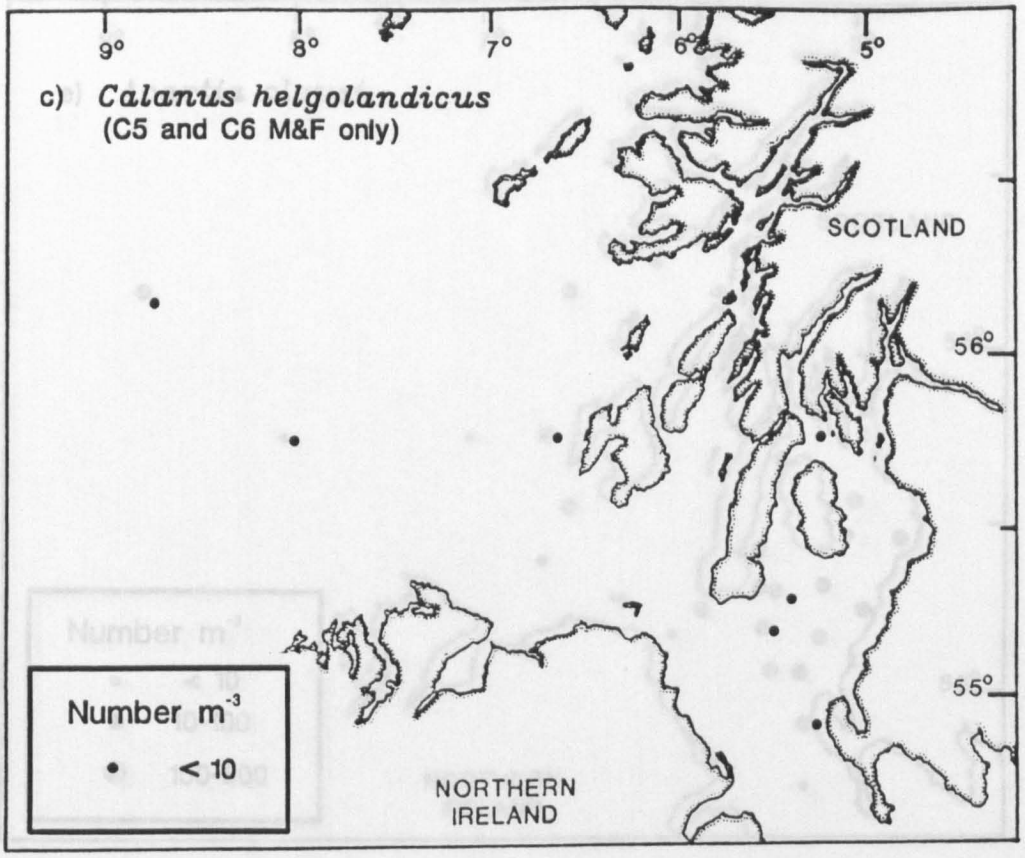


Figure 4.18 (Continued). Distribution of *Calanus* spp. (a) and *Calanus finmarchicus*, stages C5 and C6 only, (b) collected at 30m in March 1987.



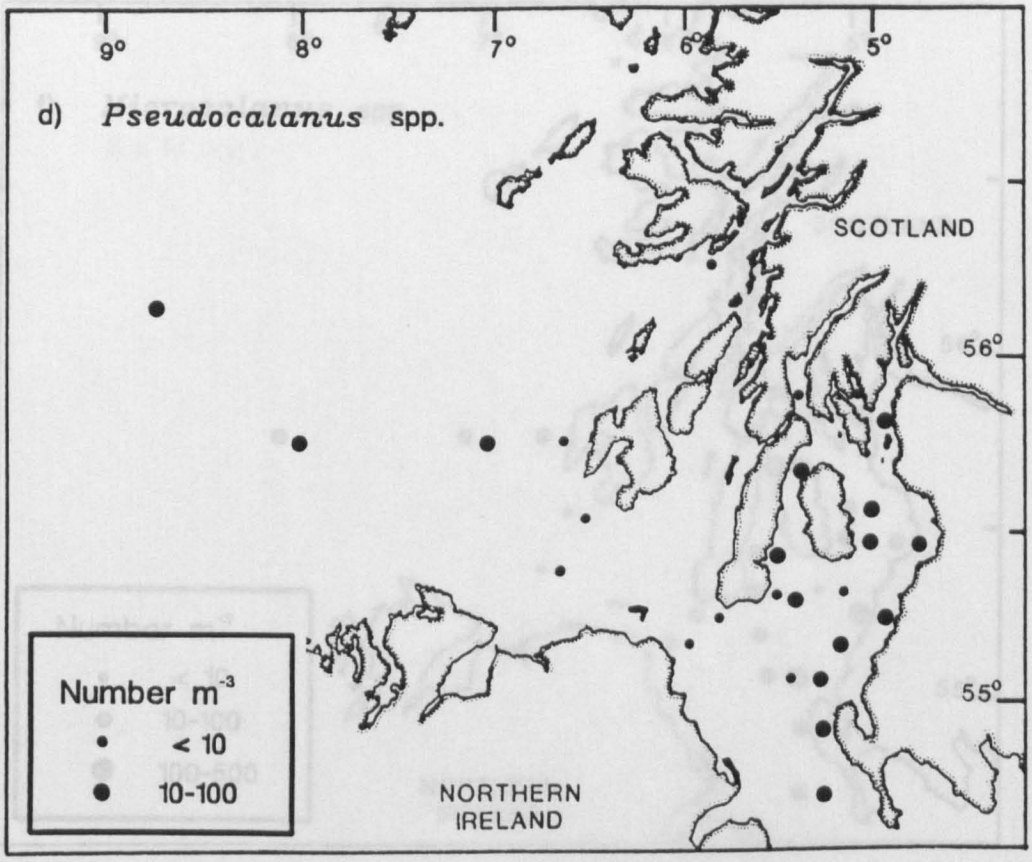
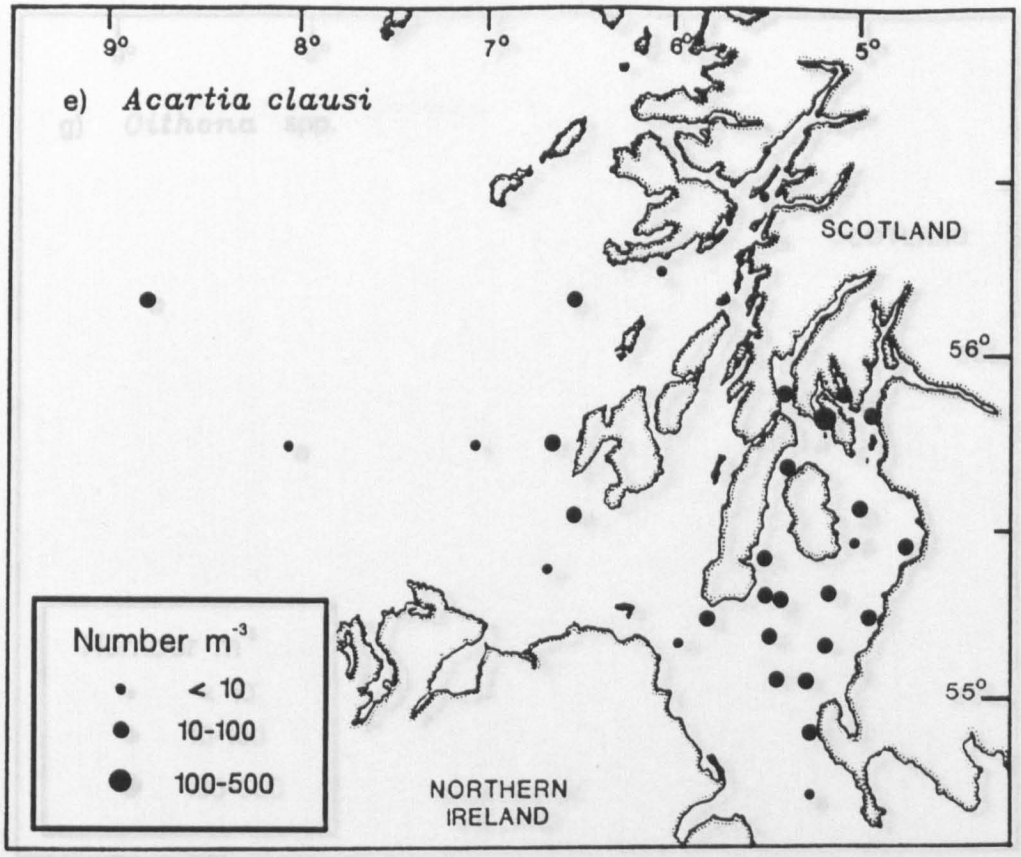


Figure 4.18 (Continued). Distribution of *Calanus helgolandicus*, stages C5 and C6 only, (c) and *Pseudocalanus* spp. (d) collected at 30m in March 1987.



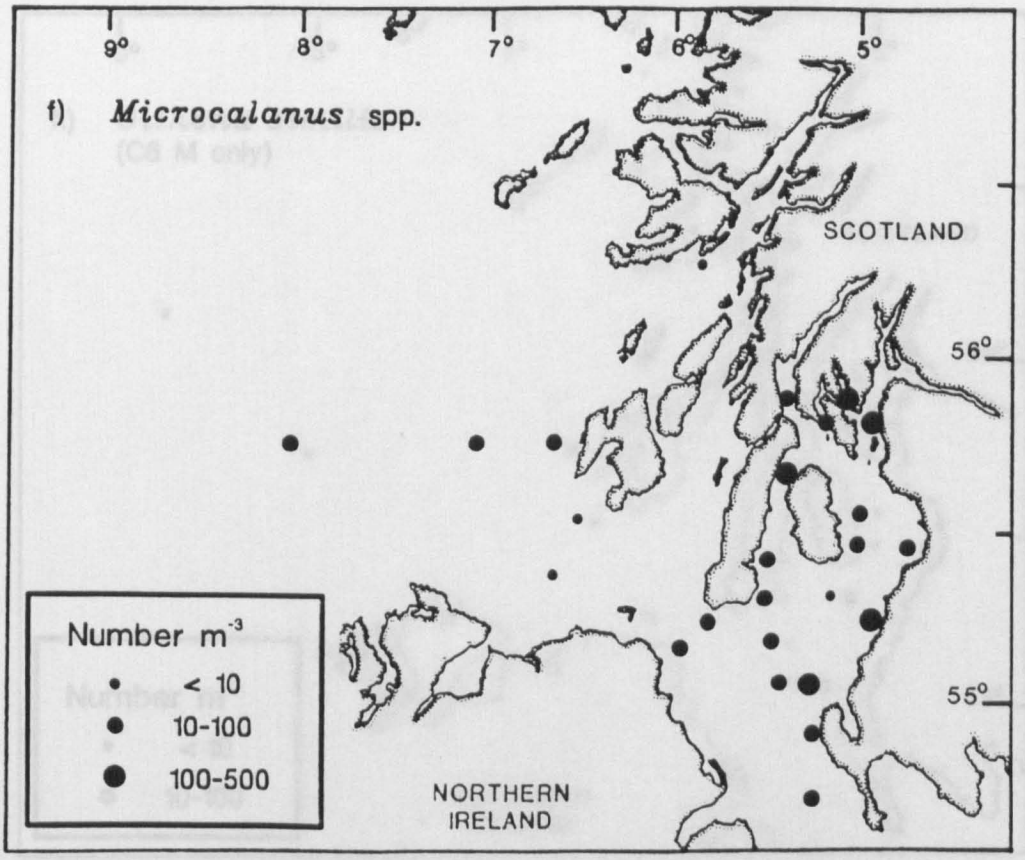
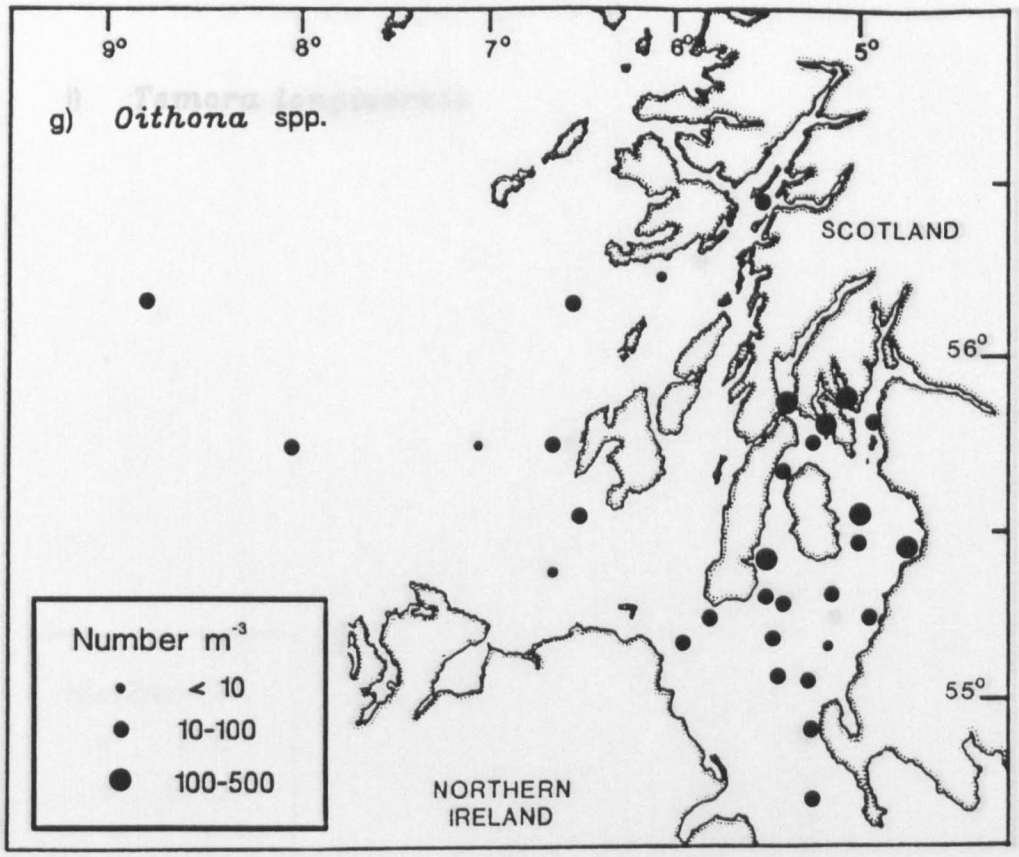


Figure 4.18 (Continued). Distribution of *Acartia clausi* (e) and *Microcalanus* spp. (f) collected at 30m in March 1987.



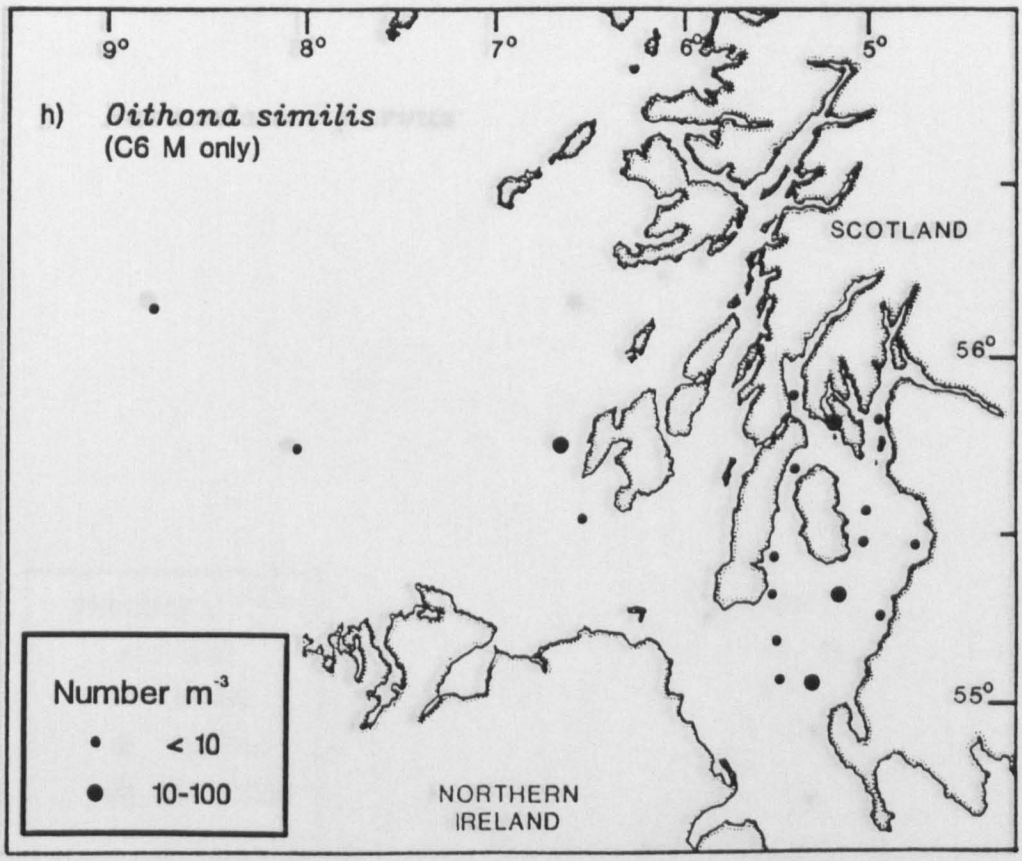
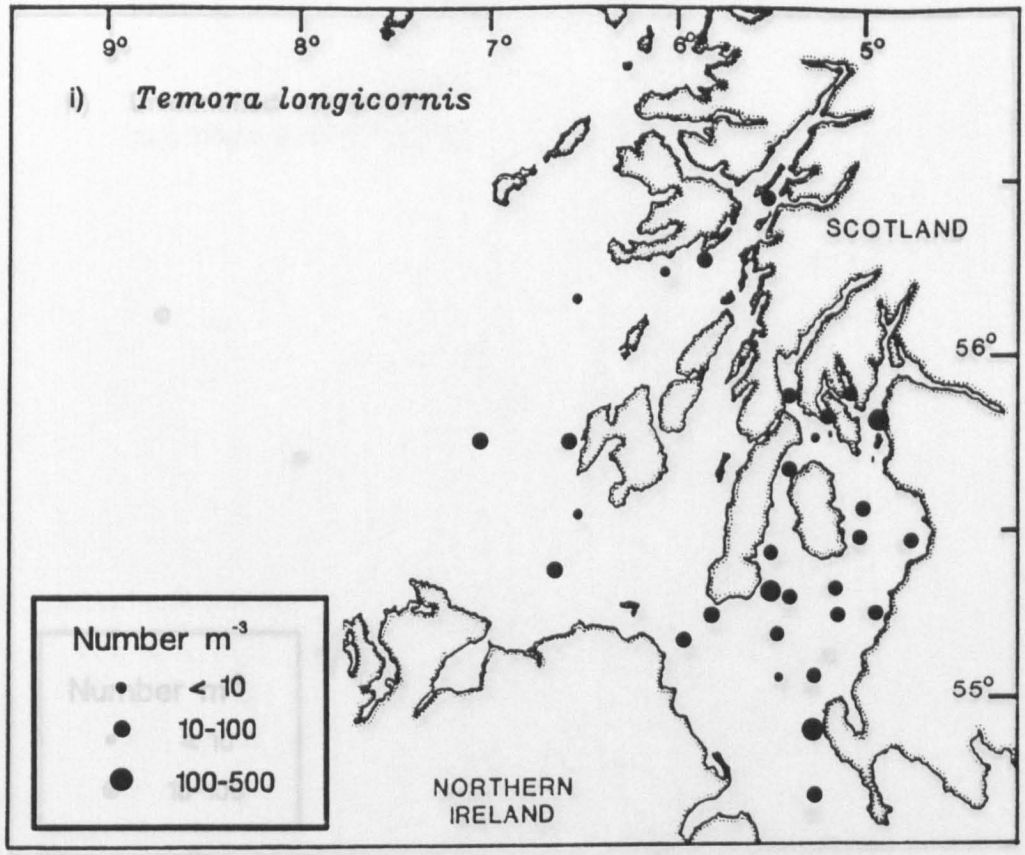


Figure 4.18 (Continued). Distribution of *Oithona* spp. (g) and *Oithona similis*, C6 males only, (h) collected at 30m in March 1987.



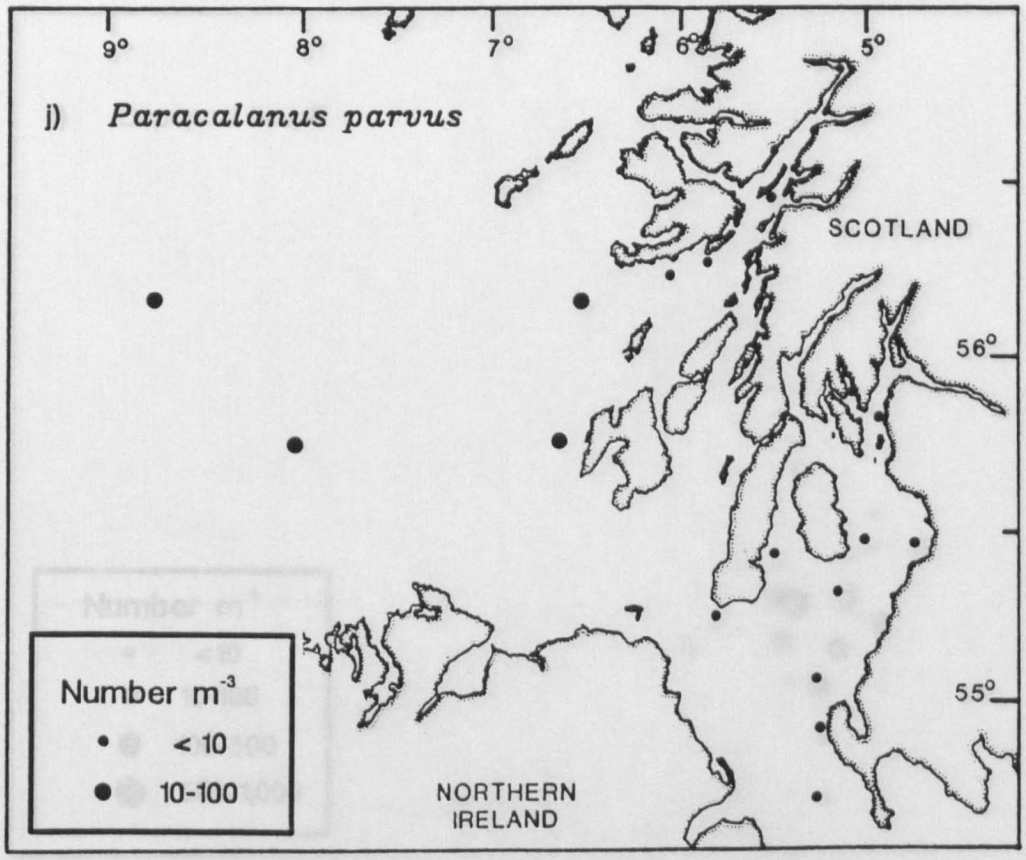
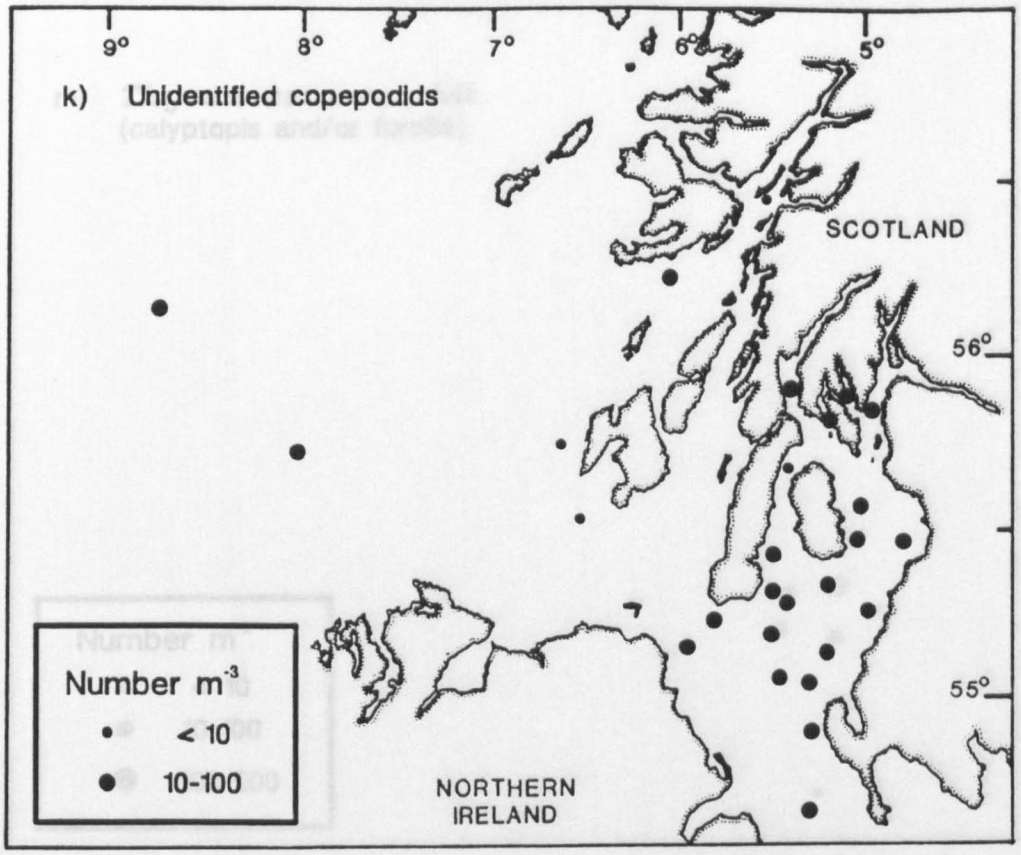


Figure 4.18 (Continued). Distribution of *Temora longicornis* (i) and *Paracalanus parvus* (j) collected at 30m in March 1987.



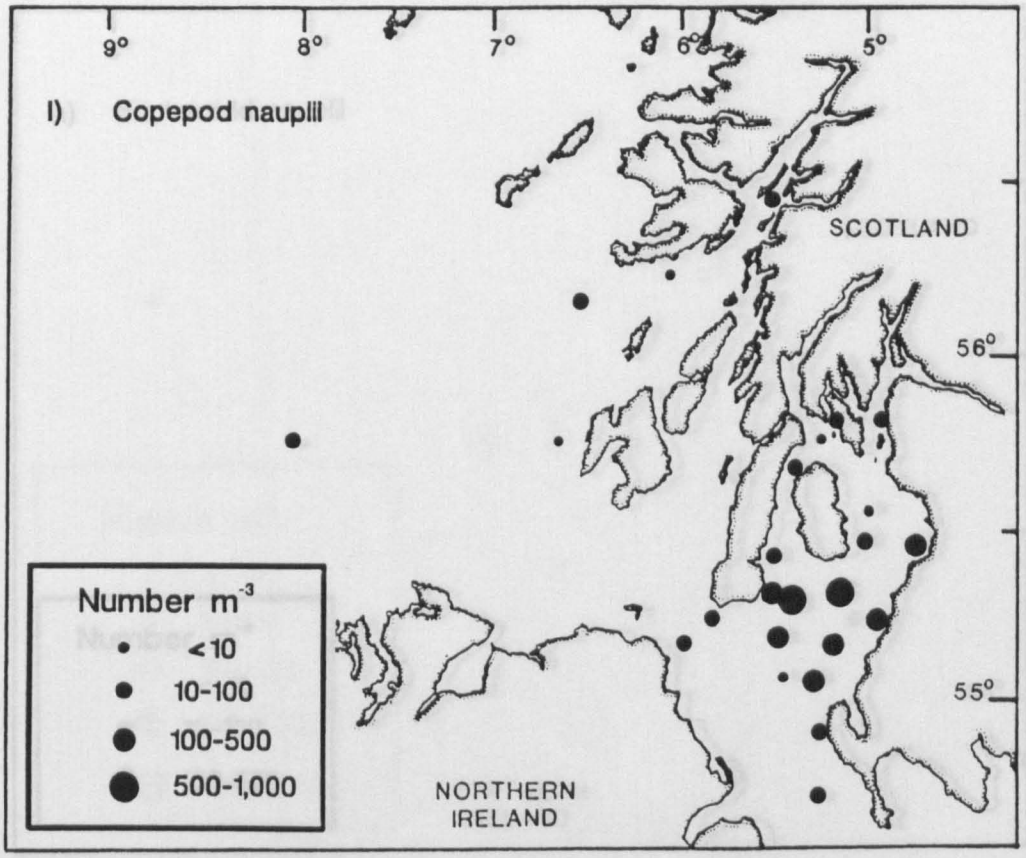
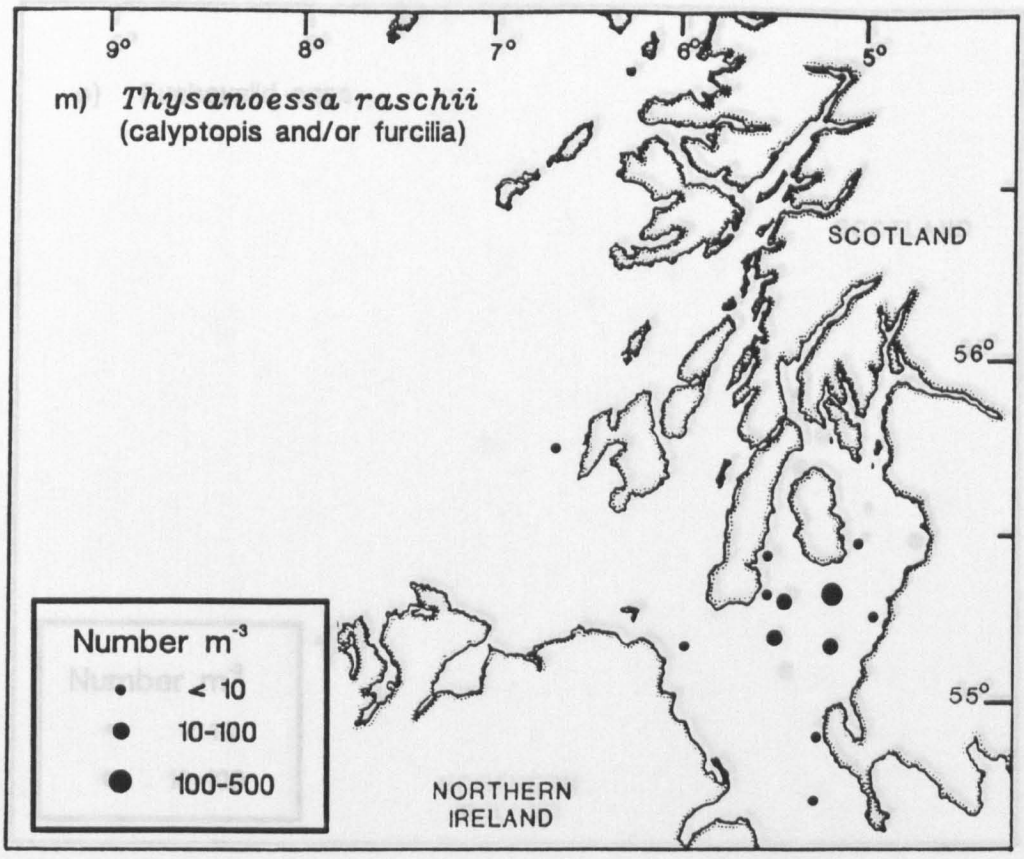


Figure 4.18 (Continued). Distribution of unidentified copepodids (k) and copepod nauplii (l) collected at 30m in March 1987.



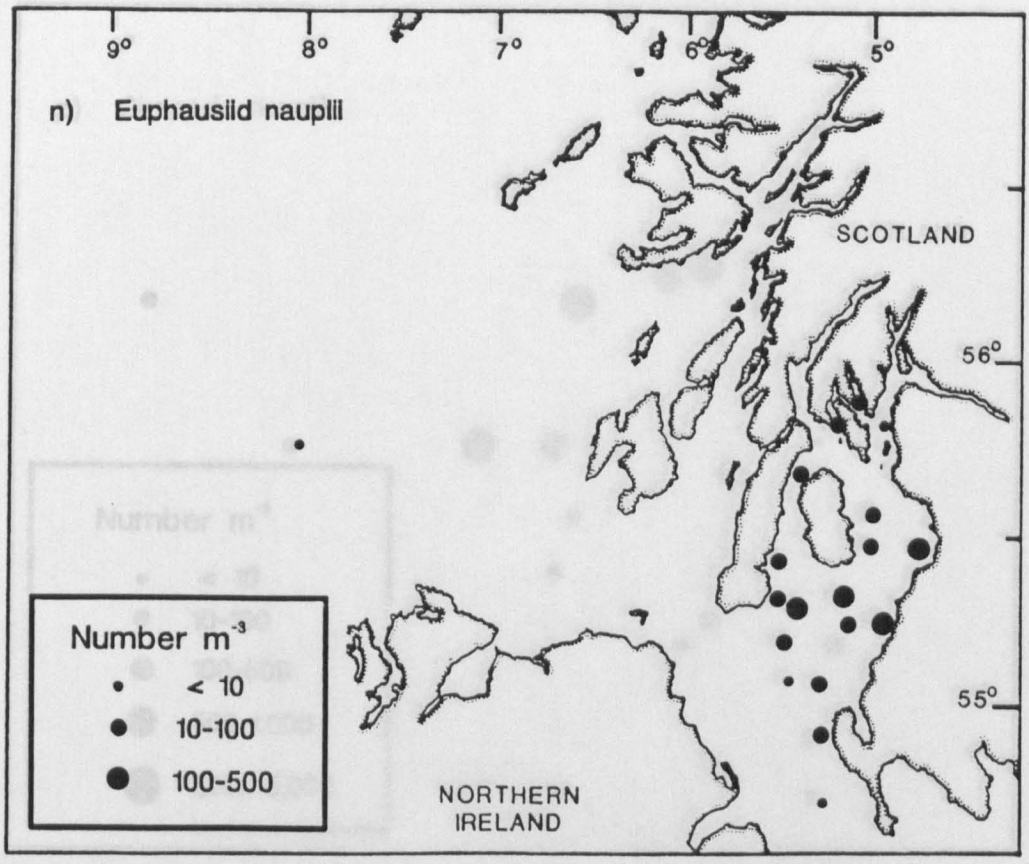
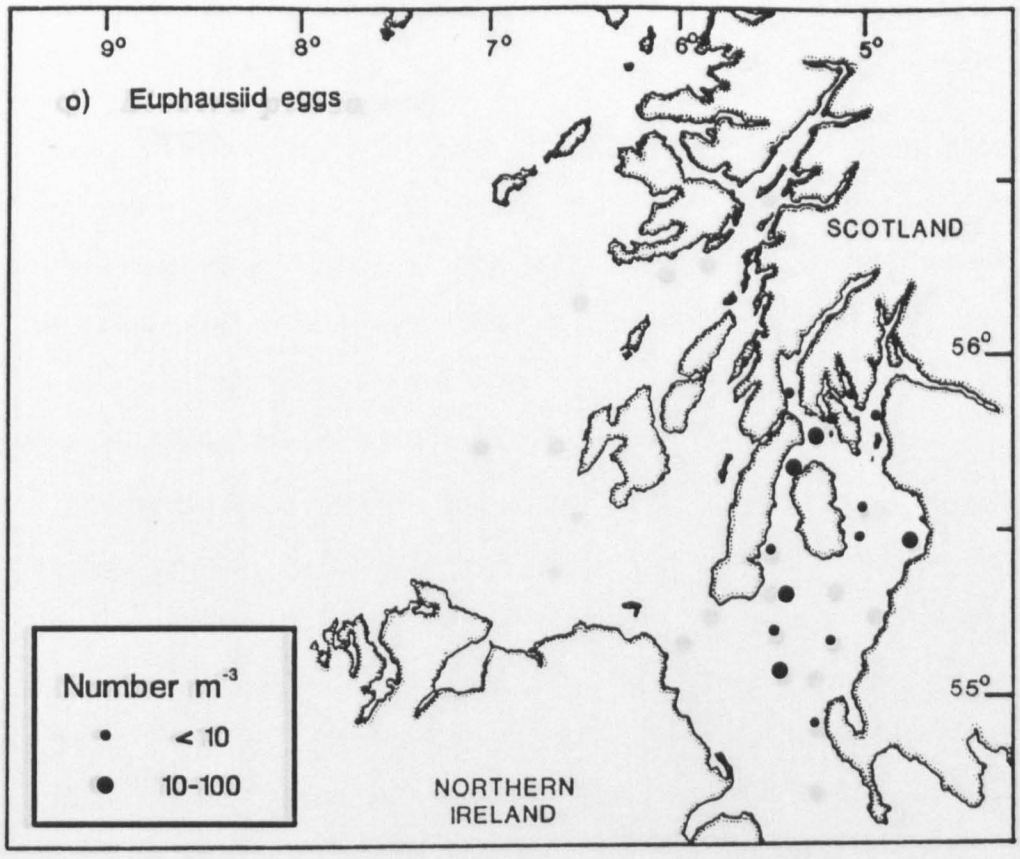


Figure 4.18 (Continued). Distribution of *Thysanoessa raschii*, calyptopis and/or furcilia, (m) and euphausiid nauplii (n) collected at 30m in March 1987.



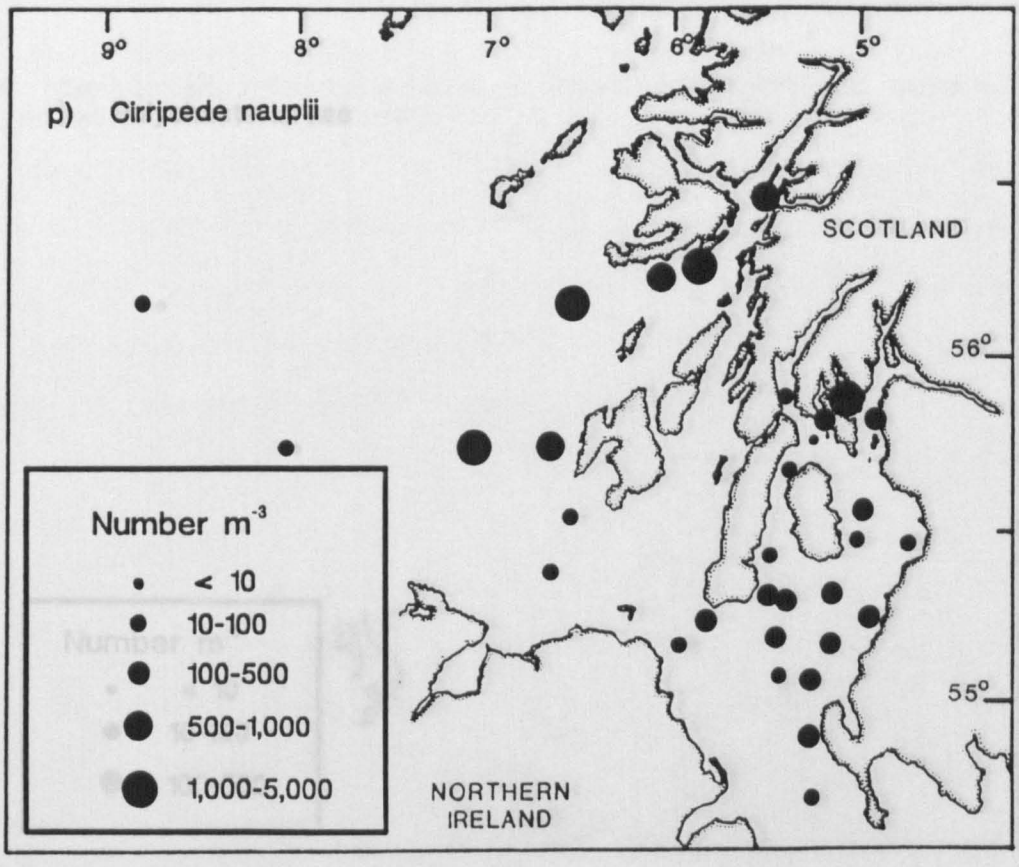
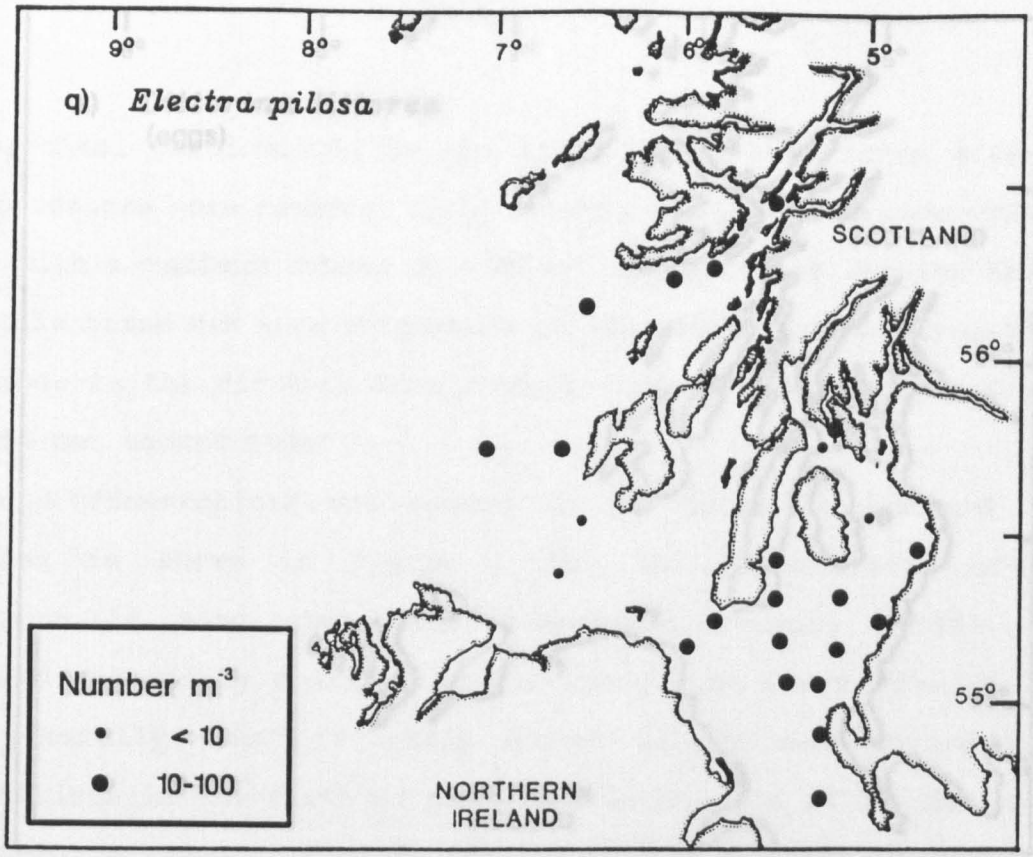


Figure 4.18 (Continued). Distribution of euphausiid eggs (o) and cirripede nauplii (p) collected at 30m in March 1987.



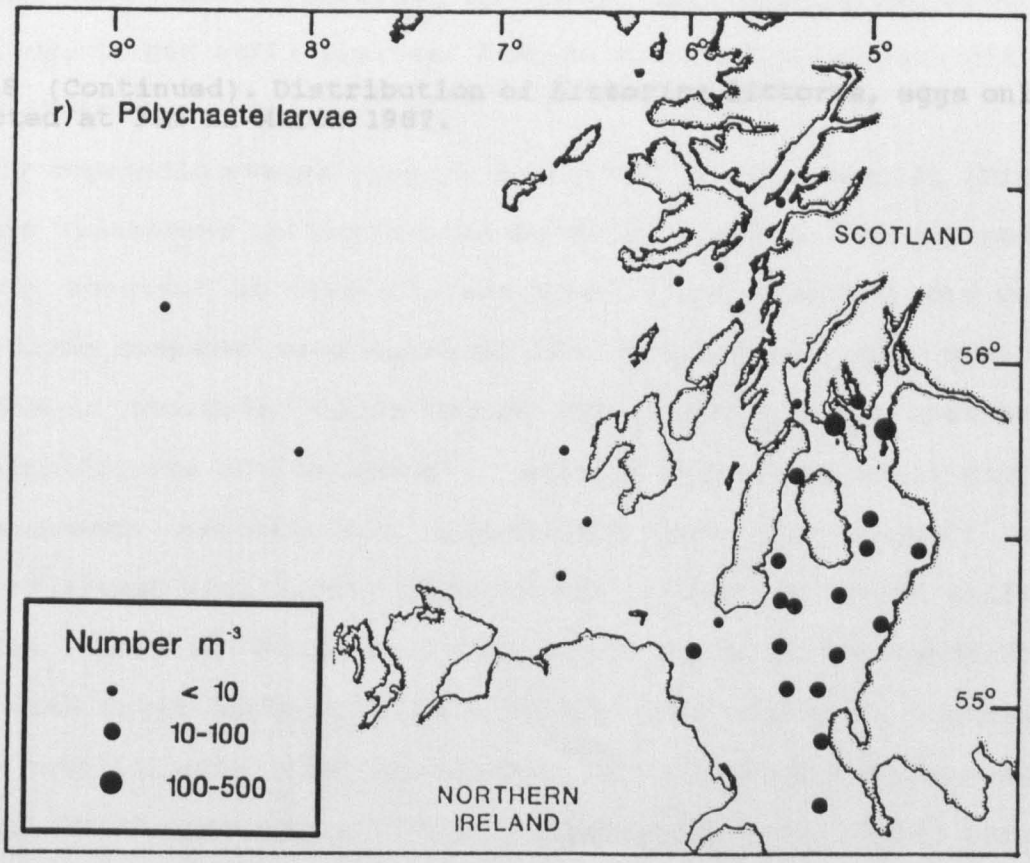


Figure 4.18 (Continued). Distribution of *Electra pilosa* (q) and polychaete larvae (r) collected at 30m in March 1987.

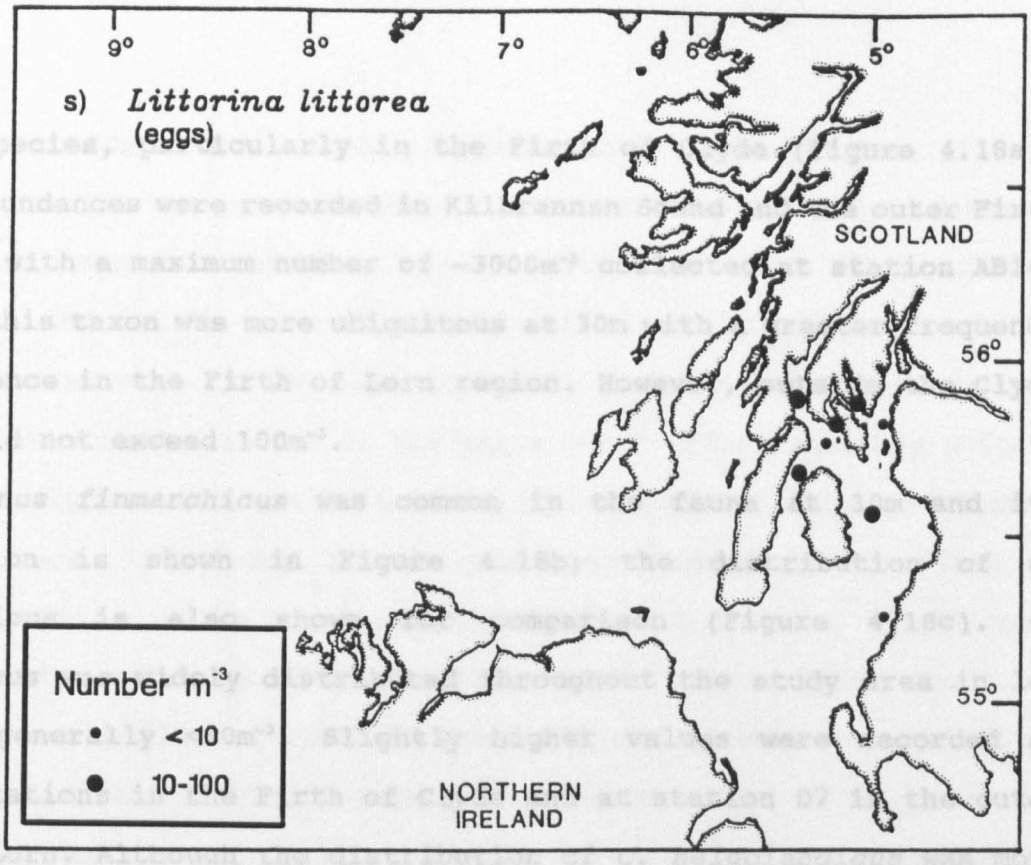


Figure 4.18 (Continued). Distribution of *Littorina littorea*, eggs only, (s) collected at 30m in March 1987.

copepod species, particularly in the Firth of Clyde (Figure 4.18a). Highest abundances were recorded in Kilbrannan Sound and the outer Firth of Clyde, with a maximum number of ~3000m^{-3} collected at station AB14. Overall, this taxon was more ubiquitous at 30m with a greater frequency of occurrence in the Firth of Lorn region. However, outside the Clyde numbers did not exceed 100m^{-3}.

Calanus finmarchicus was common in the fauna at 30m and its distribution is shown in Figure 4.18b; the distribution of *C. helgolandicus* is also shown for comparison (Figure 4.18c). *C. finmarchicus* was widely distributed throughout the study area in low numbers, generally <10m^{-3}. Slightly higher values were recorded at several stations in the Firth of Clyde and at station D7 in the outer Firth of Lorn. Although the distribution of *C. helgolandicus* was more widespread than that observed at 10m, in comparison with *C. finmarchicus*, it was still limited. Numbers of *C. helgolandicus* did not exceed 10 individuals m^{-3}.

Early copepodid stages (Figure 4.18k) and copepod nauplii (Figure 4.18l) were widespread throughout the study area. Numbers of copepodids were fairly constant at <100 m^{-3}, and numbers were less in the outer Firth of Clyde compared with those at 10m. Nauplii were most abundant at stations in the outer Clyde region with lower numbers elsewhere. Copepod nauplii were not collected at station FL0 on the Malin Shelf.

Thysanoessa raschii and euphausiid eggs and nauplii were distributed almost exclusively in the Firth of Clyde (Figures 4.18m, n and o). The centre of abundance for *T. raschii* was in the outer Firth of Clyde with small numbers (<10m^{-3}) in the North Channel. Euphausiid eggs and nauplii were more widespread throughout the Clyde, again attributable to the presence of *Meganyctiphanes norvegica*. Small numbers of nauplii were collected offshore at station D0.

Meroplankton was represented by cirripede nauplii, *Electra pilosa*, polychaete larvae, and *Littorina littorea*. Cirripede nauplii were widely

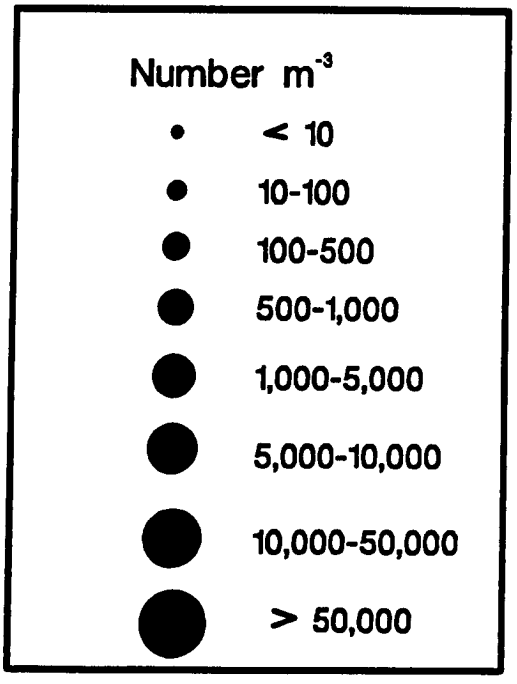
distributed at 30m with a peak of abundance in the Firth of Lorn (Figure 4.18p) similar to the pattern observed at 10m (Figure 4.17p). Numbers at 30m were comparable to those recorded at 10m; in the Firth of Lorn between ~ 5 and $20x10^2m^{-3}$, in the Clyde $<500m^{-3}$ except at station AB35A where numbers were $\sim 1.2x10^2m^{-3}$, and generally $<100m^{-3}$ in the North Channel and at the outermost stations on the Malin Shelf. *Electra pilosa* (Figure 4.18q) and polychaete larvae (Figure 4.18r) were also widely distributed in low numbers. Polychaete larvae were concentrated in the Firth of Clyde, especially in the inner regions, but small numbers, $<10m^{-3}$, were detected as far offshore as stations FL0 and D0 on the Malin Shelf. *E. pilosa* was not collected west of about 7°W and numbers were similar, $<100m^{-3}$, in both the Firths of Lorn and Clyde. Finally, *L. littorea* was fairly localized in distribution, with numbers $<100m^{-3}$, collected mainly from the inner Firth of Clyde, and at a single station in the Firth of Lorn (Figure 4.18s).

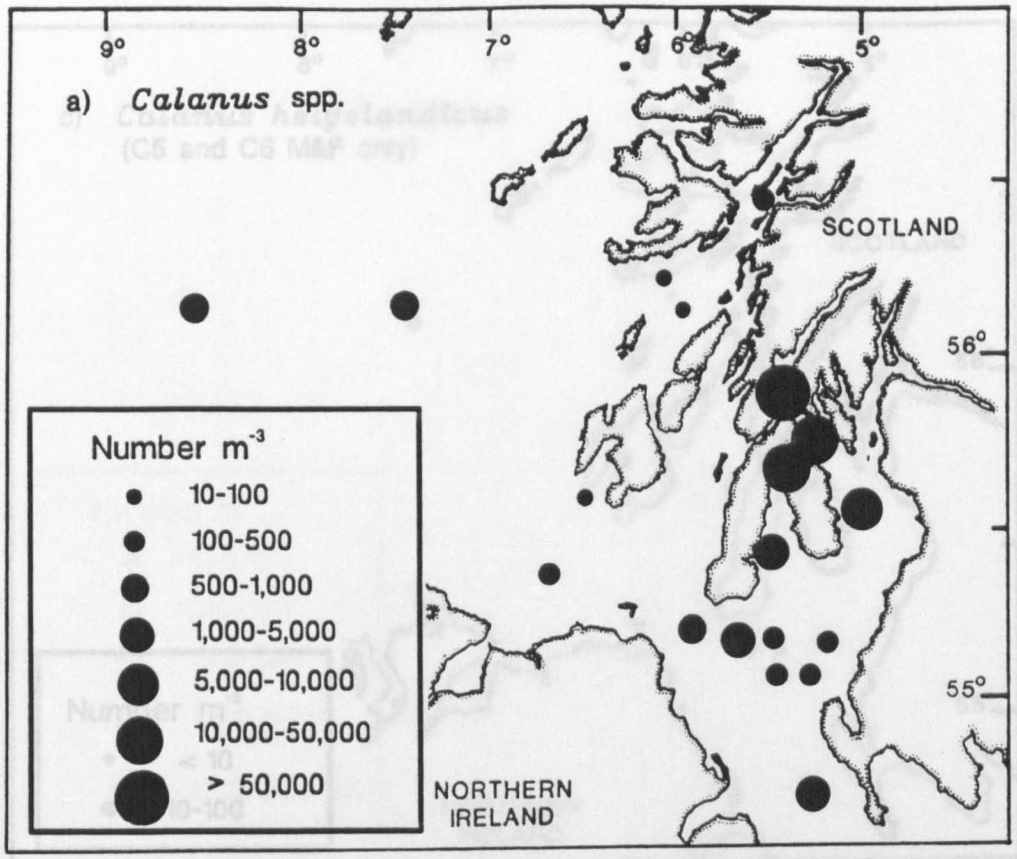
4.2.2.3 May 1986: 10m

The overall species composition of the fauna in May was similar to that in March although there were shifts in the relative abundances of many species. Nineteen of the 51 species or other taxa identified were designated 'common': eight copepods, two cladocerans, two gelatinous zooplankters and a mixture of holo- and meroplanktonic forms (Table 4.6).

Several species of copepods were widespread in distribution, with high abundances: *Calanus* spp. (Figure 4.19a), *Pseudocalanus* spp. (Figure 4.19d), *Acartia clausi* (Figure 4.19e), and *Oithona* spp. (Figure 4.19g). Although numbers varied among stations, centres of abundance for the above species, with the exception of *Oithona* spp., were concentrated in the inner Firth of Clyde in the vicinity of Loch Fyne and/or around the Island of Arran. Numbers in these regions were at least 10^4m^{-3}; higher

Figure 4.19 Distribution of 'common' species collected at stations sampled at 10m in May 1986. The full range of values used in this figure is shown below.





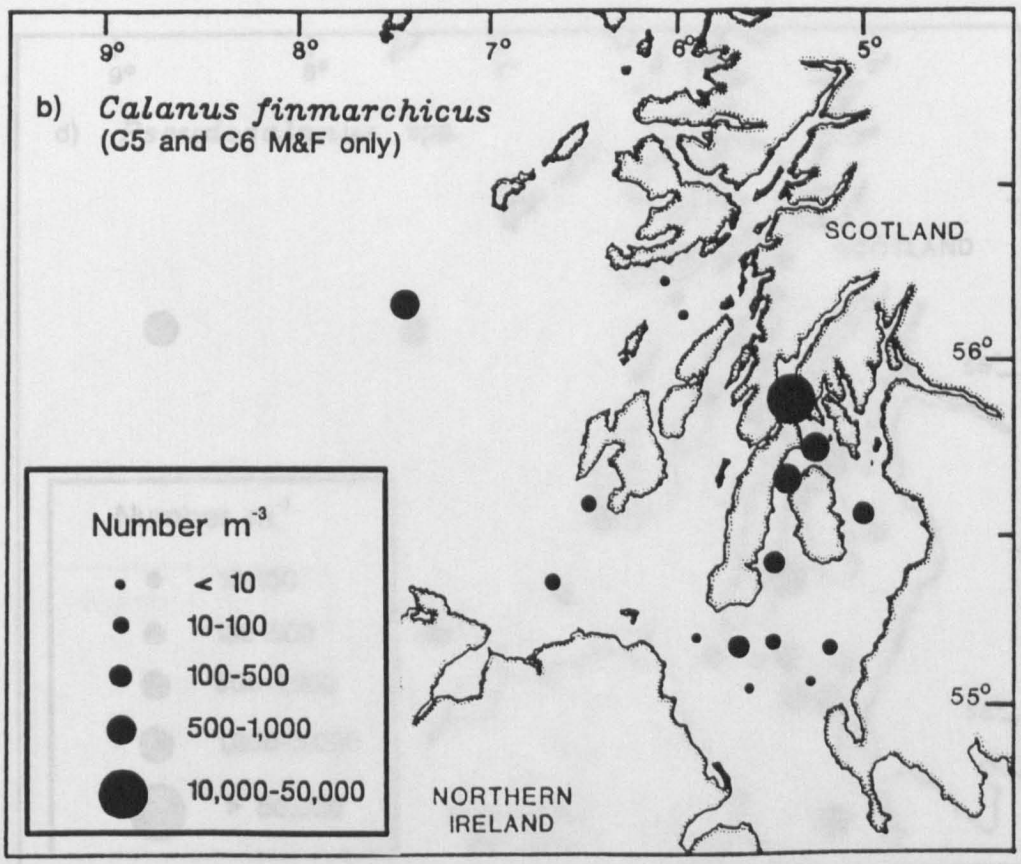


Figure 4.19 (Continued). Distribution of *Calanus* spp. (a) and *Calanus finmarchicus*, stages C5 and C6 only, (b) collected at 10m in May 1986.

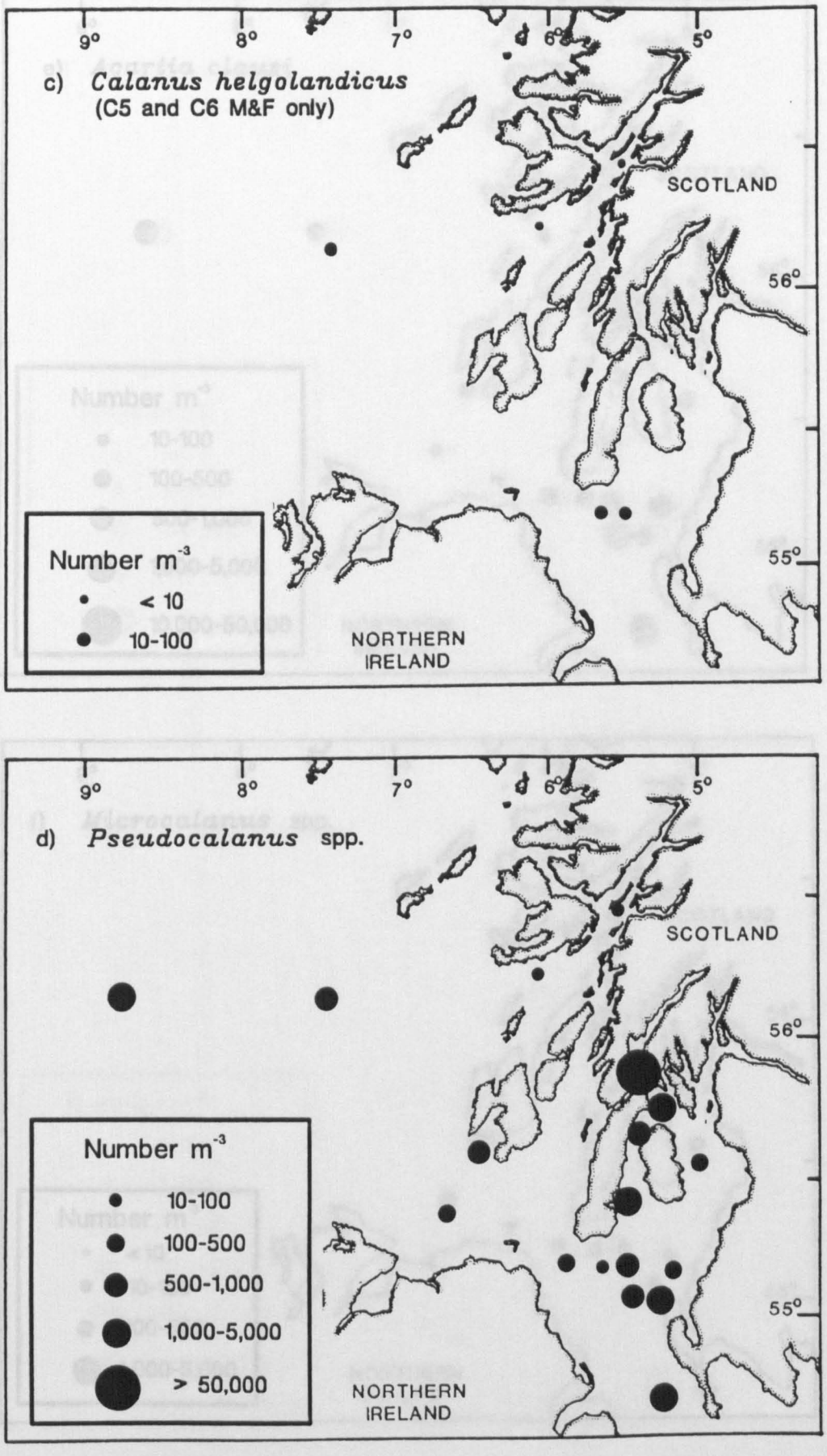
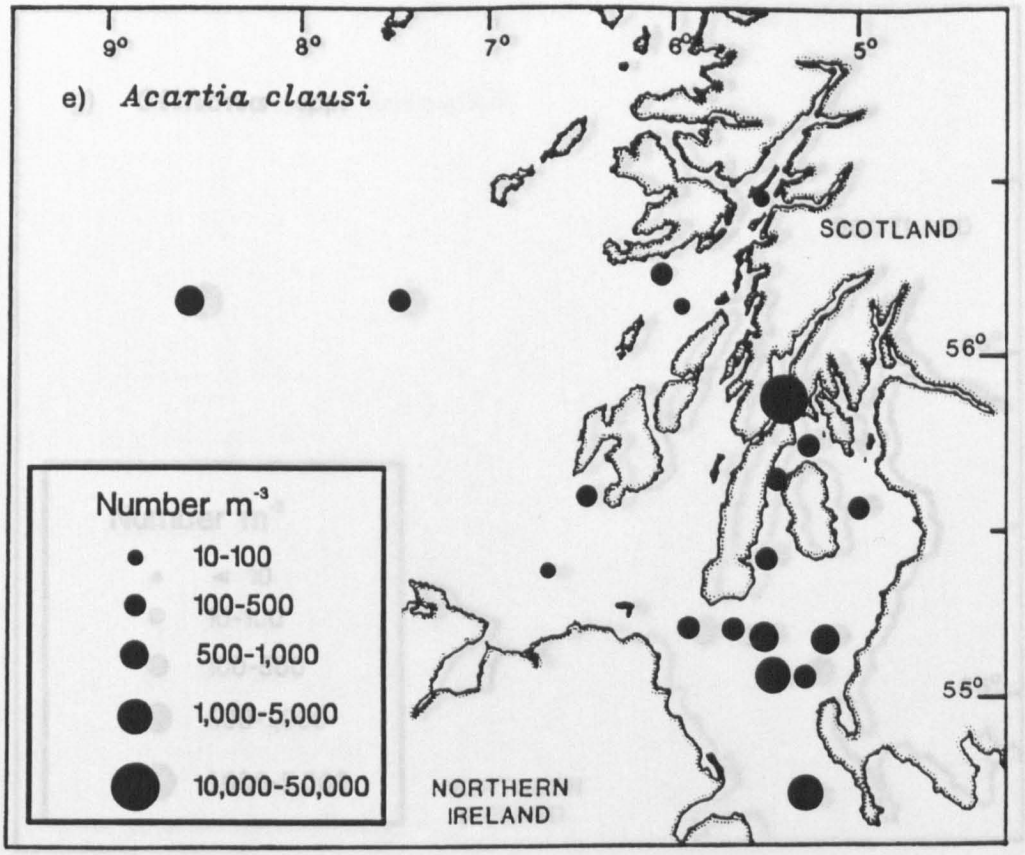


Figure 4.19 (Continued). Distribution of *Calanus helgolandicus*, stages C5 and C6 only, (c) and *Pseudocalanus* spp. (d) collected at 10m in May 1986.



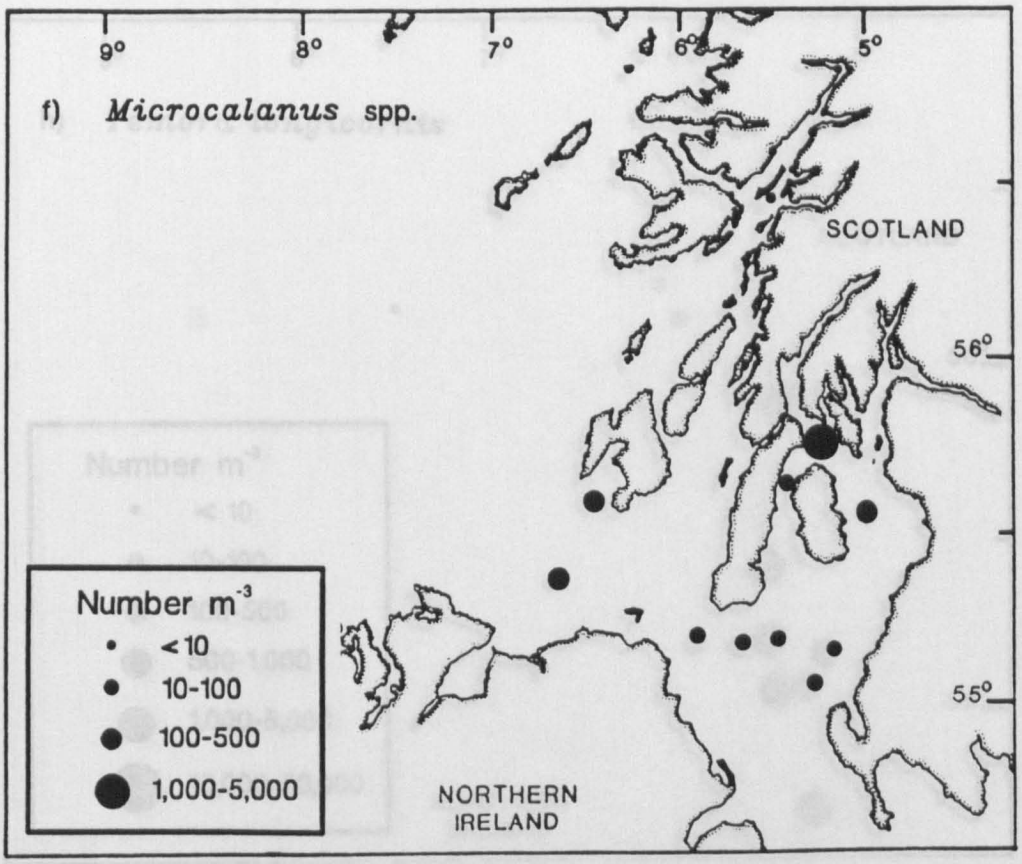
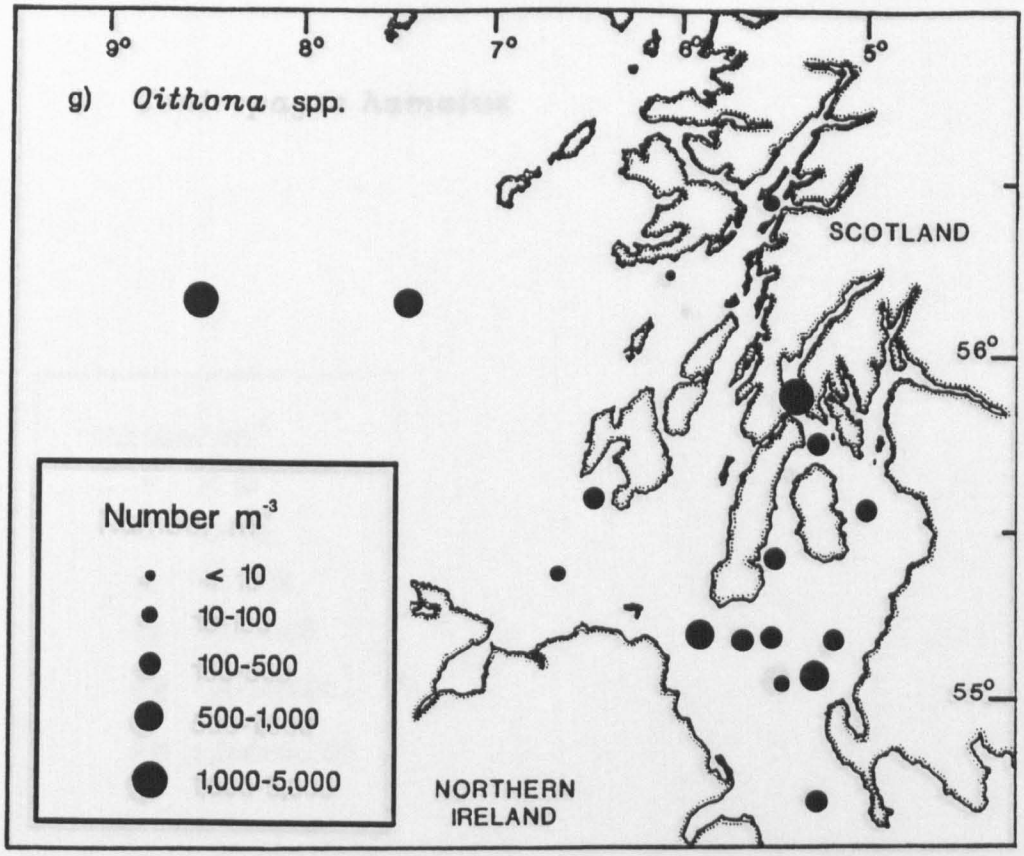


Figure 4.19 (Continued). Distribution of *Acartia clausi* (e) and *Microcalanus* spp. (f) collected at 10m in May 1986.



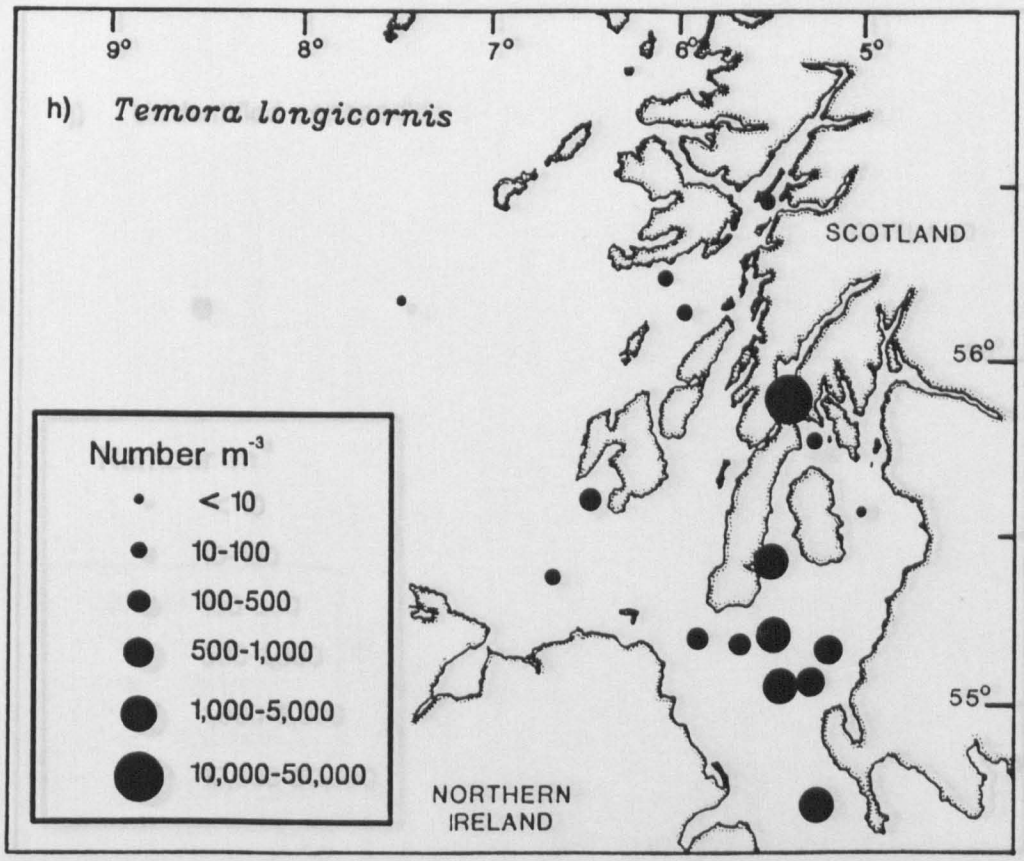
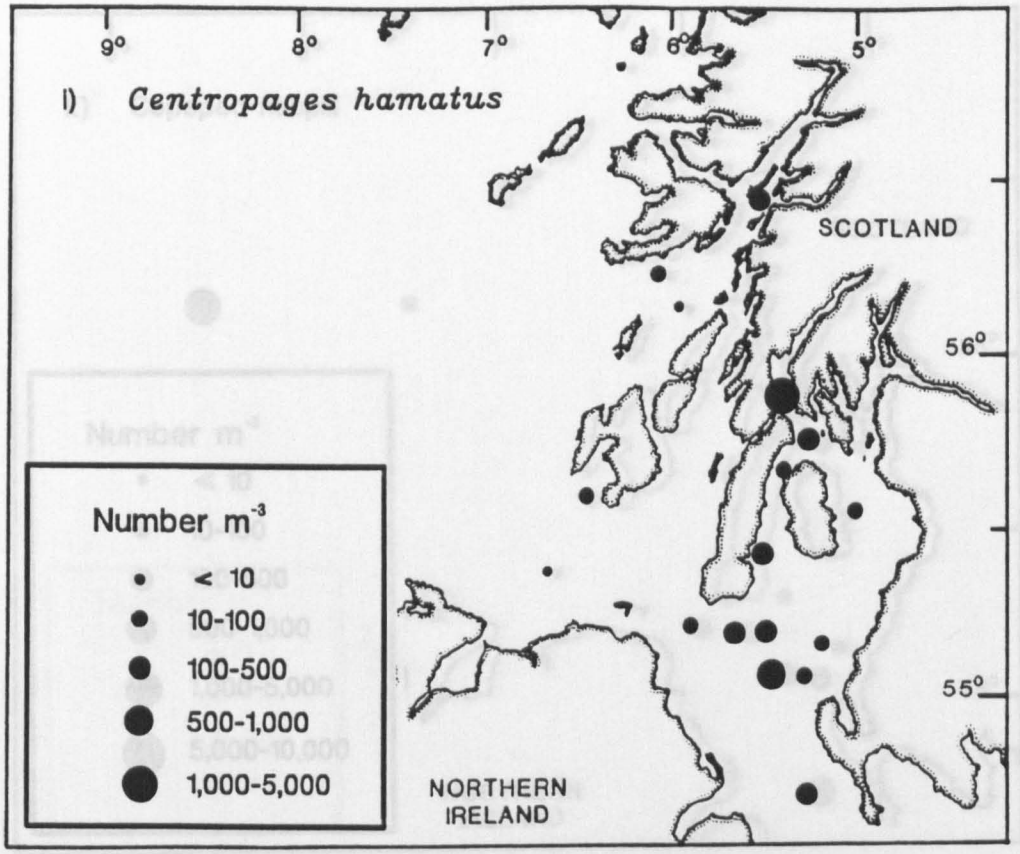


Figure 4.19 (Continued). Distribution of *Oithona* spp. (g) and *Temora longicornis*, (h) collected at 10m in May 1986.



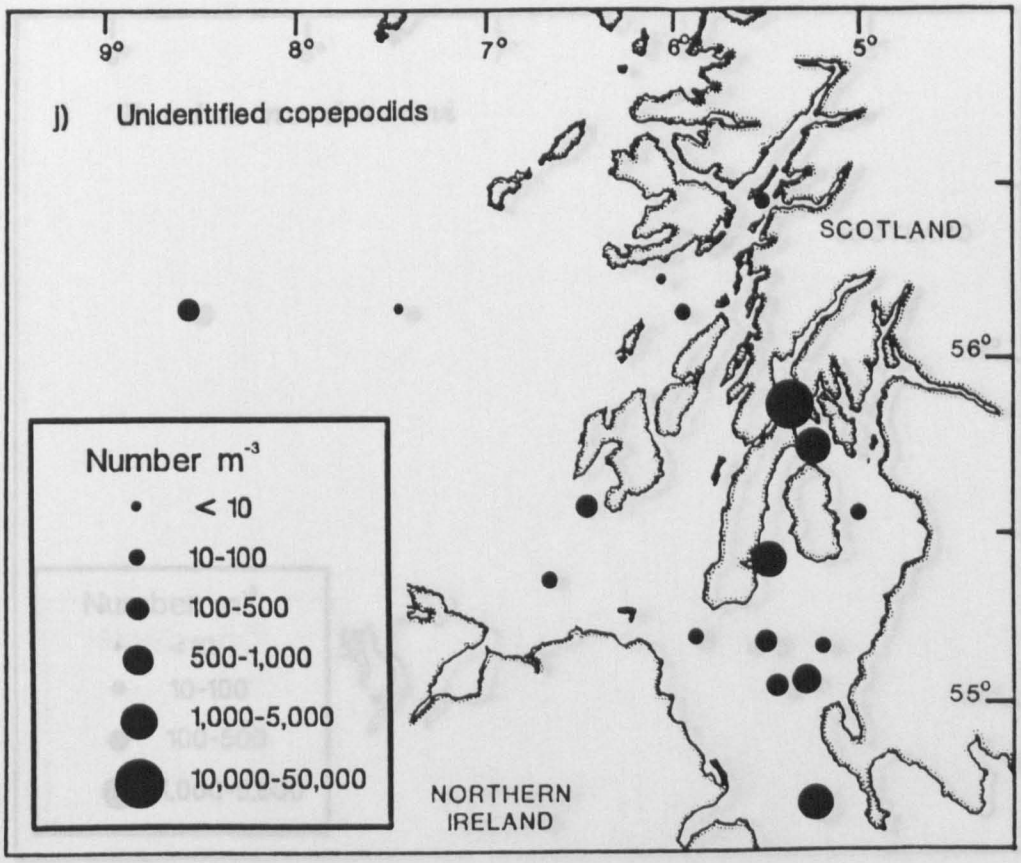
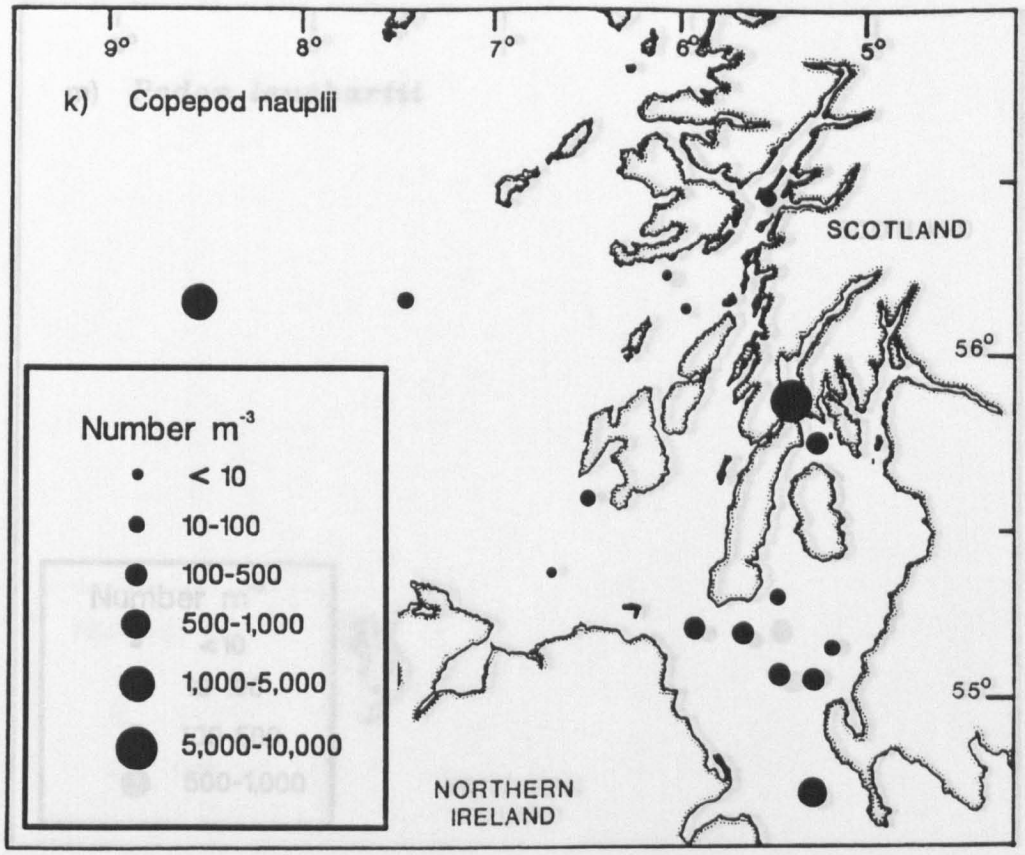


Figure 4.19 (Continued). Distribution of *Centropages hamatus* (i) and unidentified copepodids (j) collected at 10m in May 1986.



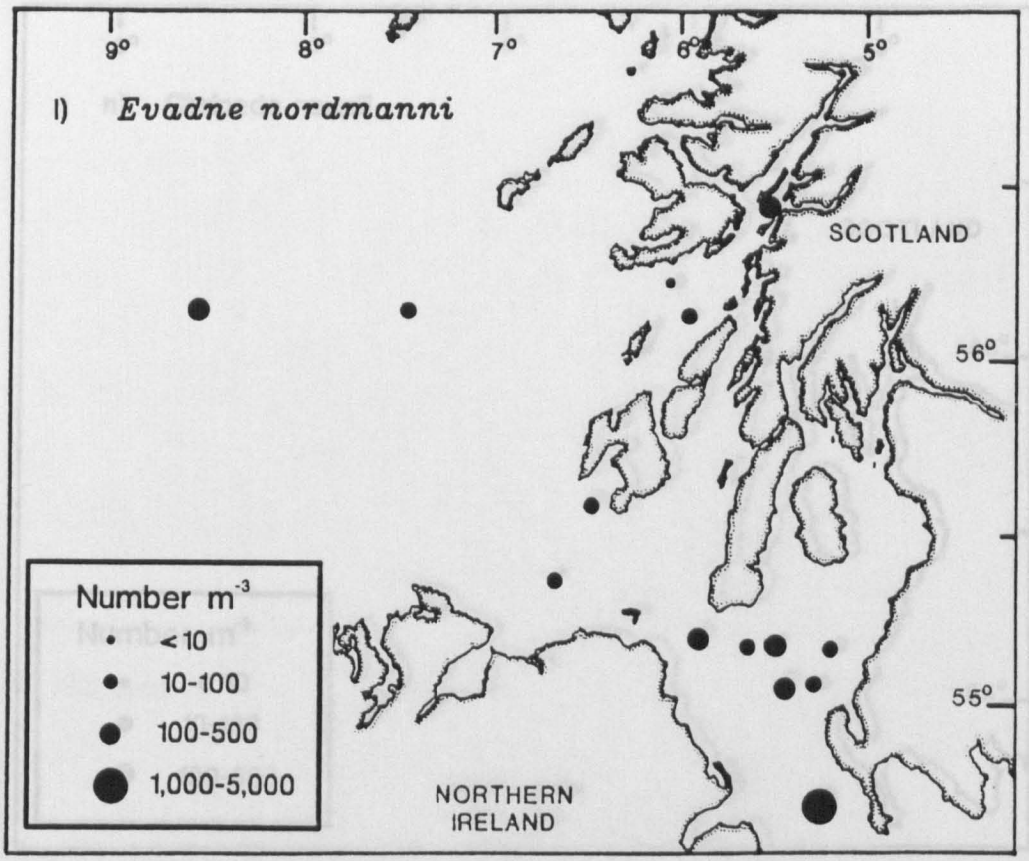
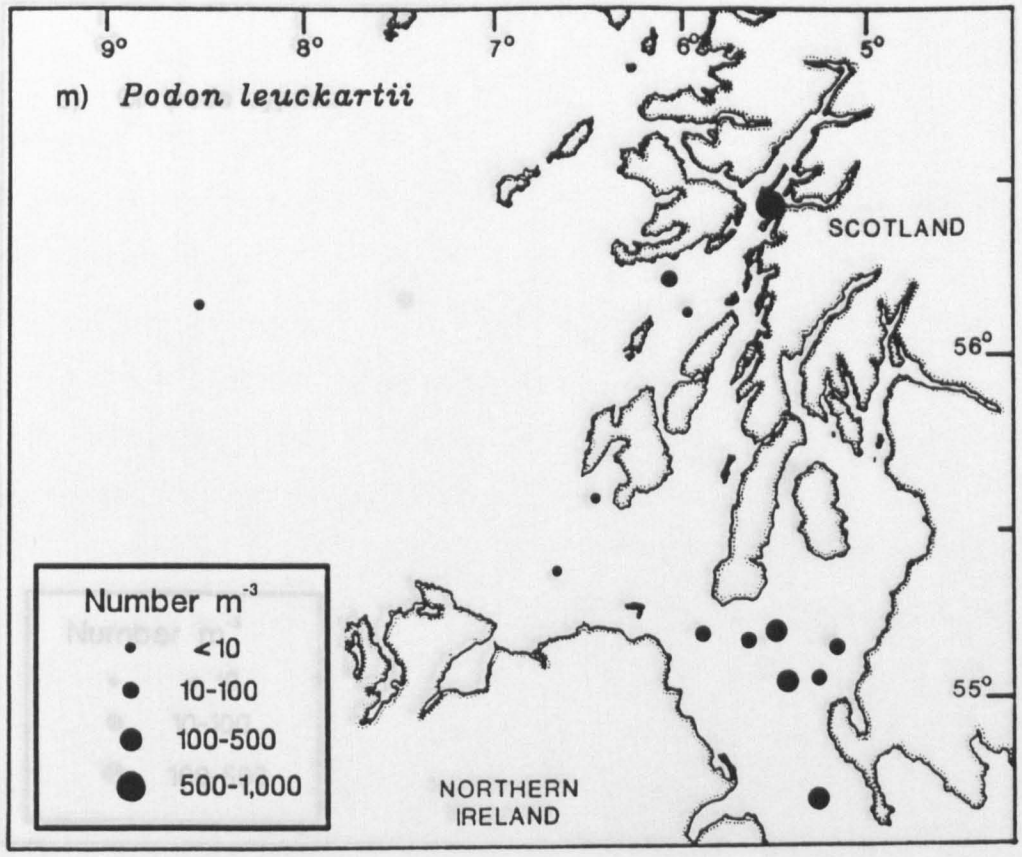


Figure 4.19 (Continued). Distribution of copepod nauplii (k) and *Evadne nordmanni* (l) collected at 10m in May 1986.



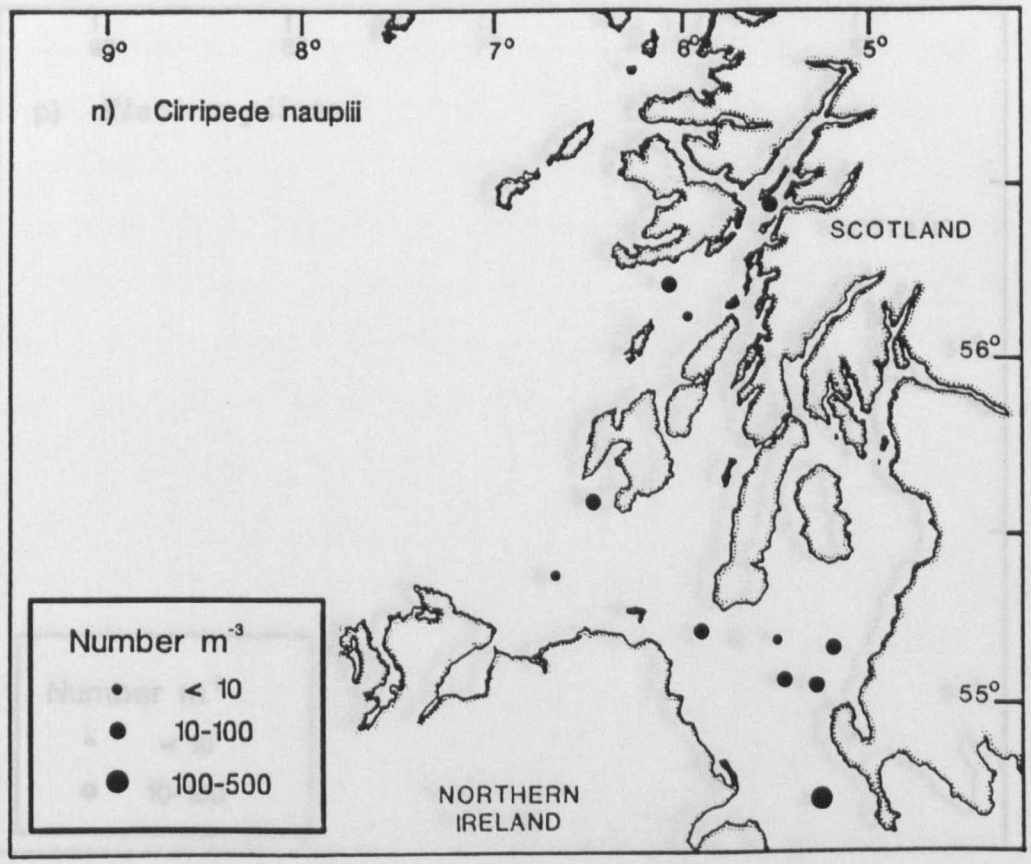
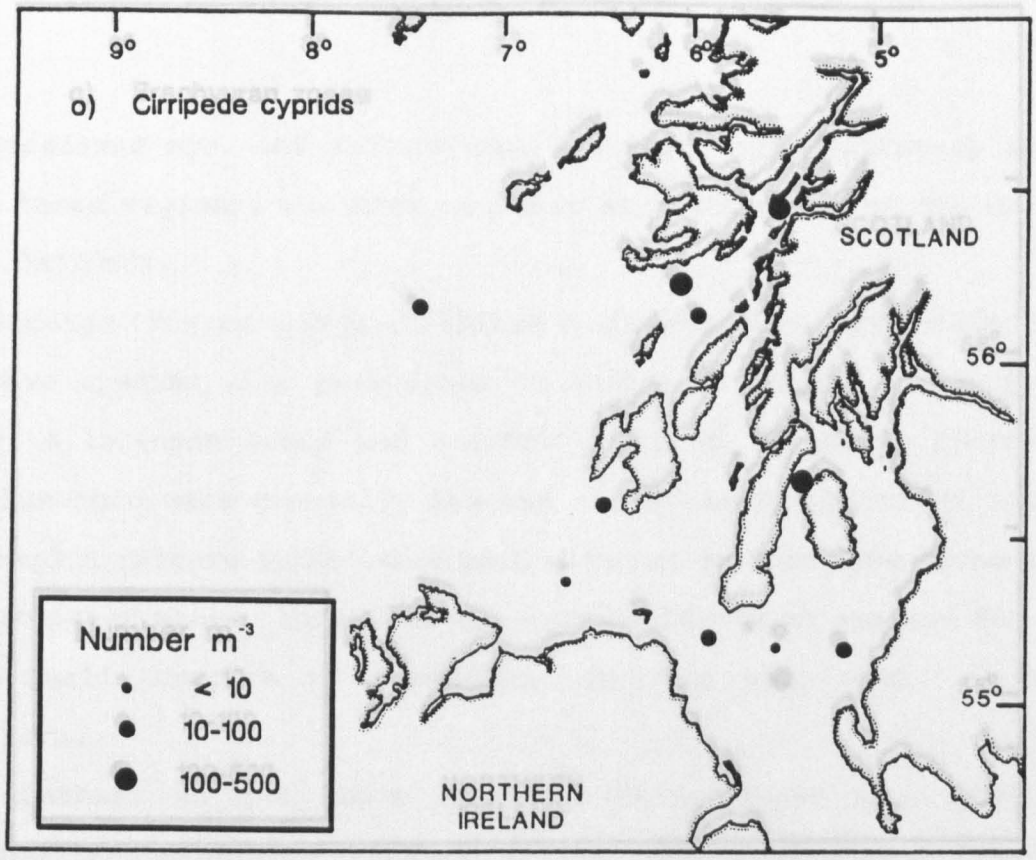


Figure 4.19 (Continued). Distribution of *Podon leuckartii*, (m) and cirripede nauplii (n) collected at 10m in May 1986.



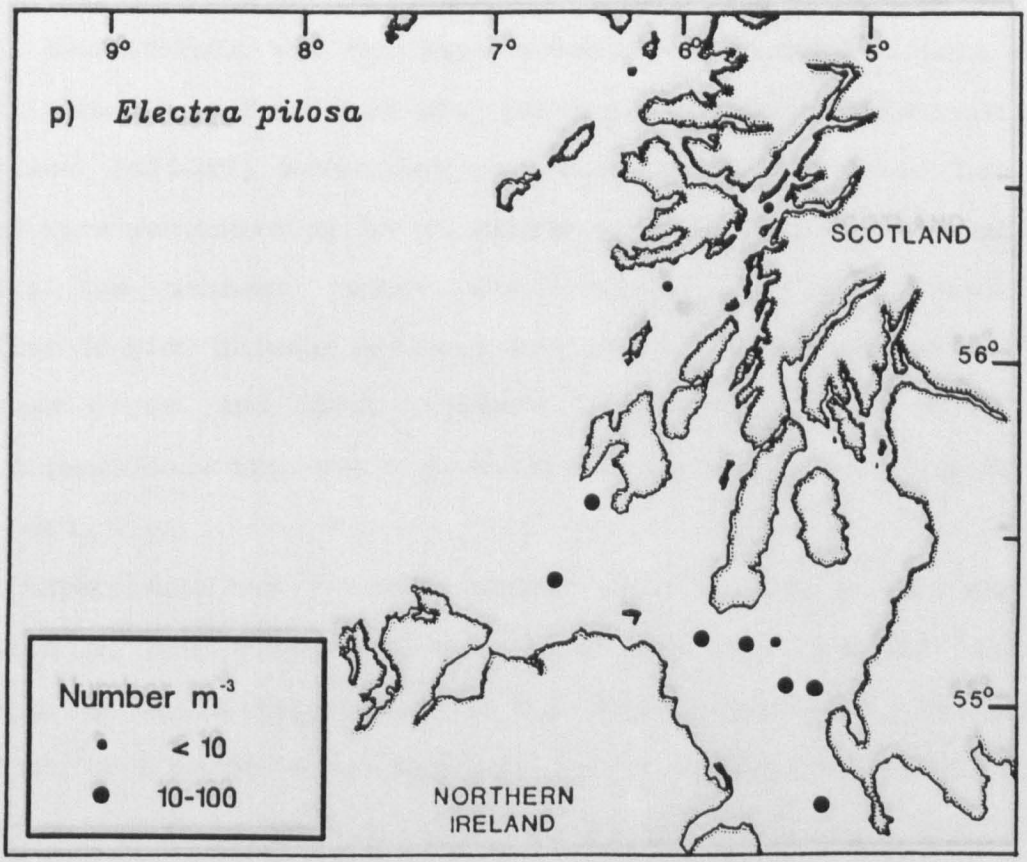
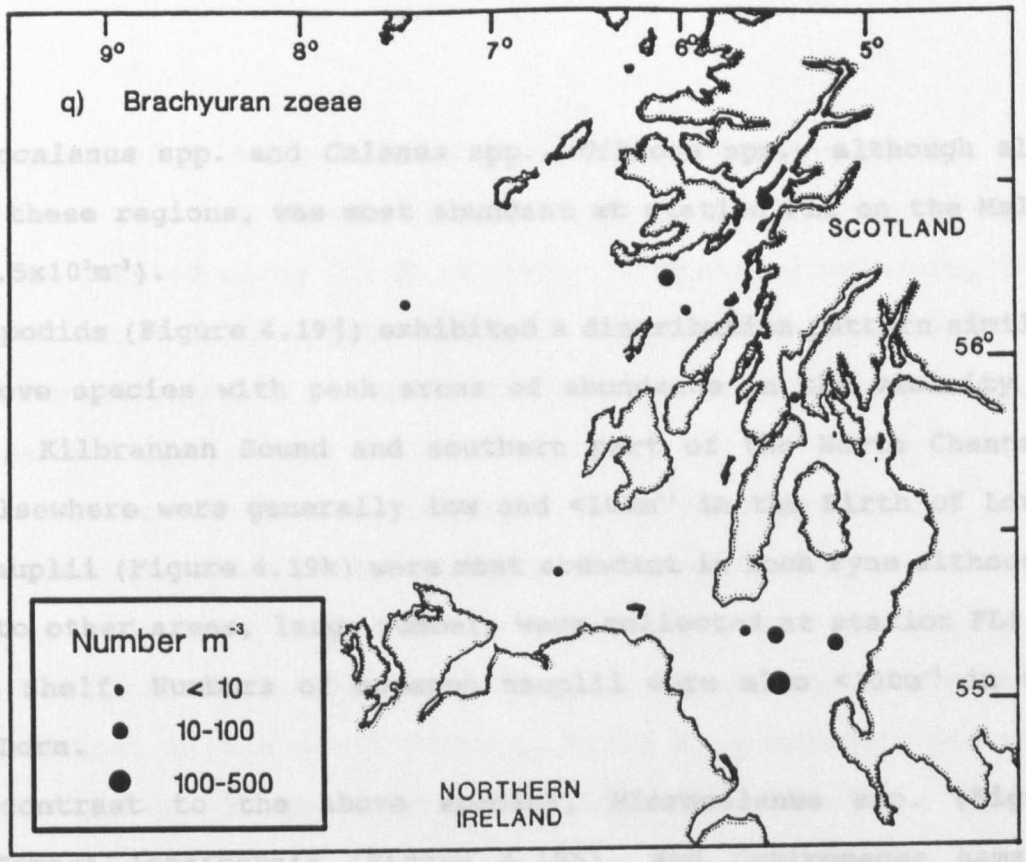


Figure 4.19 (Continued). Distribution of cirripede cyprids (o) and *Electra pilosa* (p) collected at 10m in May 1986.



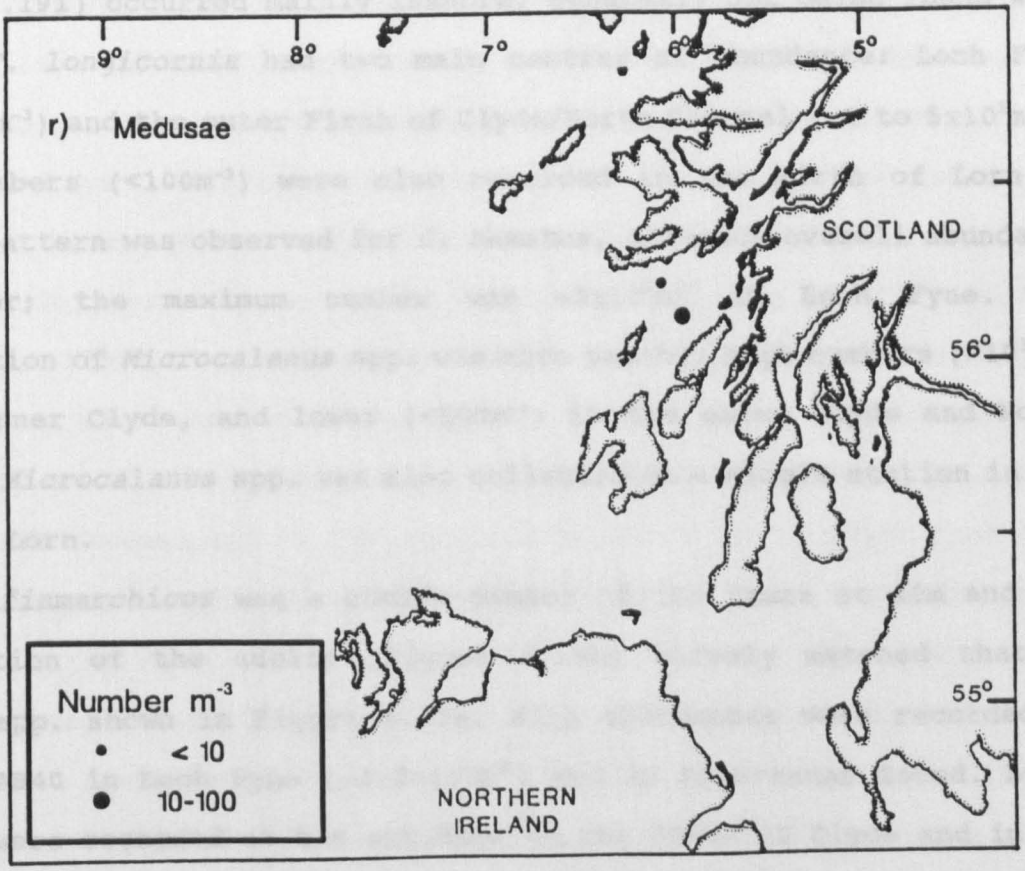


Figure 4.19 (Continued). Distribution of Brachyuran zoeae (q) and Medusae (r) collected at 10m in May 1986.

for *Pseudocalanus* spp. and *Calanus* spp.. *Oithona* spp., although also common in these regions, was most abundant at station FL1 on the Malin Shelf (~$3.5x10^3m^{-3}$).

Copepodids (Figure 4.19j) exhibited a distribution pattern similar to the above species with peak areas of abundance in the vicinity of Loch Fyne, Kilbrannan Sound and southern part of the North Channel. Numbers elsewhere were generally low and $<100m^{-3}$ in the Firth of Lorn. Copepod nauplii (Figure 4.19k) were most abundant in Loch Fyne although, relative to other areas, large numbers were collected at station FL1 on the Malin Shelf. Numbers of copepod nauplii were also $<100m^{-3}$ in the Firth of Lorn.

In contrast to the above species, *Microcalanus* spp. (Figure 4.19f), *Temora longicornis* (Figure 4.19h), and *Centropages hamatus* (Figure 4.19i) occurred mainly inshore, generally not being found west of 7°W. *T. longicornis* had two main centres of abundance: Loch Fyne (~$3.5x10^4m^{-3}$) and the outer Firth of Clyde/North Channel (~1 to $5x10^3m^{-3}$). Lower numbers ($<100m^{-3}$) were also recorded in the Firth of Lorn. A similar pattern was observed for *C. hamatus*, although overall abundance was lower; the maximum number was ~$3x10^3m^{-3}$ in Loch Fyne. The distribution of *Microcalanus* spp. was more patchy; high numbers ($>10^3m^{-3}$) in the inner Clyde, and lower ($<500m^{-3}$) in the outer Clyde and North Channel. *Microcalanus* spp. was also collected at a single station in the Firth of Lorn.

C. finmarchicus was a common member of the fauna at 10m and the distribution of the adults (Figure 4.19b) closely matched that of *Calanus* spp. shown in Figure 4.19a. High abundances were recorded at station AB40 in Loch Fyne (~$1.2x10^4m^{-3}$) and in Kilbrannan Sound. Lower numbers were recorded at the entrance to the Firth of Clyde and in the North Channel. Numbers were higher offshore at station M3 (~$600m^{-3}$), relative to those in the contiguous Firth of Lorn, but *C. finmarchicus* was not collected at the outermost shelf station, FL0. In comparison,

the distribution of *C. helgolandicus* was patchy, occurring at only five of the nineteen stations sampled (Figure 4.19c). Interestingly, three of these were located along the FL transect of stations extending from the Firth of Lorn onto the Malin Shelf. *C. helgolandicus* also occurred at two stations located at the entrance to the Firth of Clyde. Numbers collected were $<100m^{-3}$ at all stations.

The cladocerans, *Evadne nordmanni* and *Podon leuckartii* (G.O. Sars), although collected in March (Table 4.6), were common members of the fauna only in May. Both species were collected from all areas excluding the inner Firth of Clyde (Figures 4.19l and m). *E. nordmanni* was most abundant in the North Channel, while *P. leuckartii* was most abundant in the inner Firth of Lorn. Overall the two species generally did not exceed $500m^{-3}$.

Meroplankton, represented by cirripede nauplii and cyprids, *Electra pilosa* and brachyuran zoeae, all exhibited similar distribution patterns, occurring primarily in the outer Firth of Clyde, North Channel and Firth of Lorn. Cirripede nauplii were collected in low numbers in the Firth of Lorn, North Channel and the entrance to the Firth of Clyde (Figure 4.19n), but not west of approximately 7°W. Only cyprids occurred in the inner Firth of Clyde, at station AB44 in Kilbrannan Sound (Figure 4.19o). They were also collected in the Firth of Lorn and offshore as far as station M3. *E. pilosa* (Figure 4.19p) were found inshore, mainly in the North Channel and at the entrance to the Firth of Clyde, and only in low numbers. Brachyuran zoeae were similarly distributed but more abundant in the Firth of Lorn (Figure 4.19q). Zoeae also occurred in small numbers as far west as station M3, midway to the shelf edge.

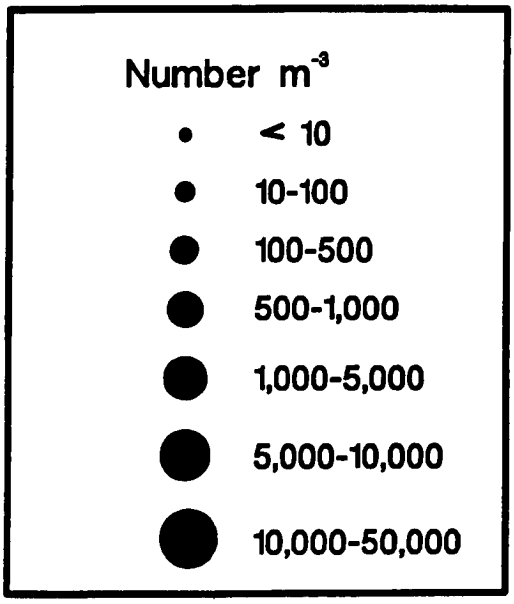
Medusae were common members of the fauna at station E4 in the Firth of Lorn (Figure 4.19r). They were collected at only one other nearby station, E2, and numbers were low ($<17m^{-3}$) at both sites.

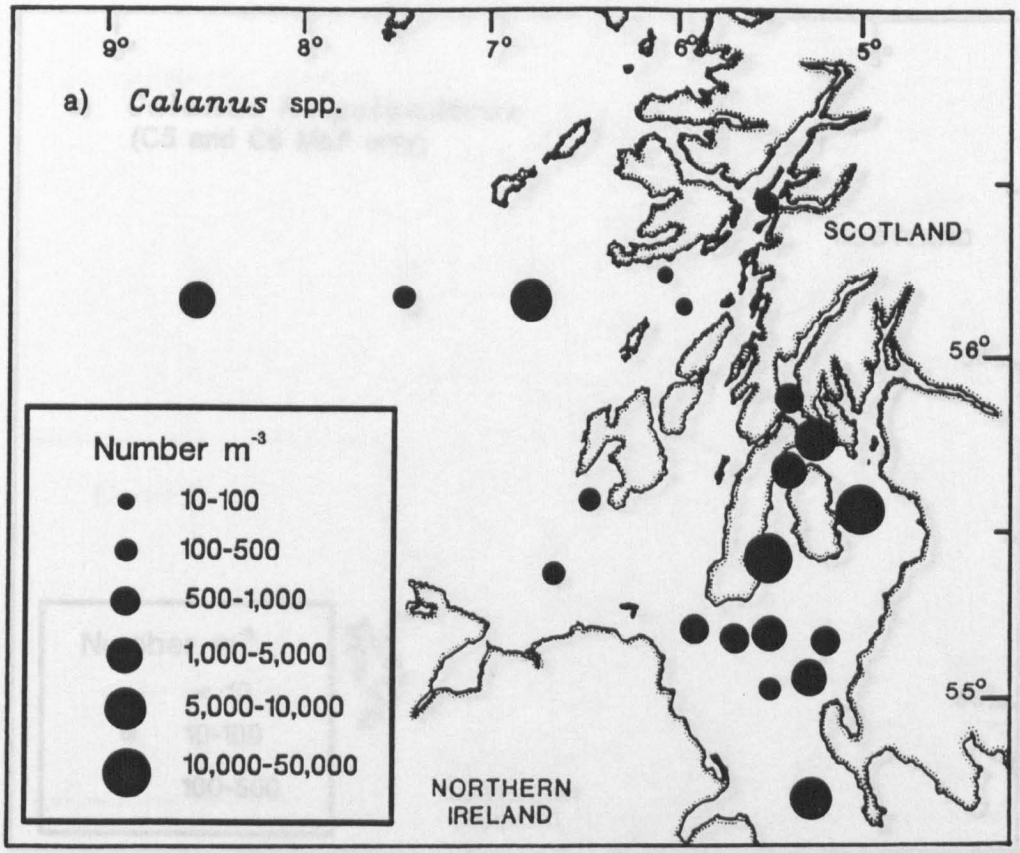
4.2.2.4 May 1986: 30m

Sixty-one species or other taxa were identified from samples collected at 30m in May. Twenty of these were 'common' members of the fauna, half of which were copepods. In general, species distributions were more widespread at 30m than at 10m. *Calanus* spp., *Pseudocalanus* spp., *Acartia clausi*, *Oithona* spp., *Temora longicornis*, and *Paracalanus parvus*, were all widely distributed throughout the study area. Overall, *Calanus* spp. were most abundant with large numbers (~$3x10^4 m^{-3}$ at AB30) collected from the inner Firth of Clyde in the region surrounding Arran (Figure 4.20a). Numbers were variable in the North Channel and on the Malin Shelf but generally low (<$500m^{-3}$) in the Firth of Lorn. *C. finmarchicus* (Figure 4.20b) exhibited a similar distribution pattern to that of *Calanus* spp. Numbers were higher in the vicinity of Arran (~$1500m^{-3}$ at AB30) and relatively low elsewhere (<$300m^{-3}$). *C. helgolandicus* was also widely distributed at 30m occurring on the Malin Shelf, in the outer Firth of Lorn, the North Channel and at two stations in the Firth of Clyde (Figure 4.20c). However, numbers remained generally low (<$10m^{-3}$) with a maximum of $119m^{-3}$ collected at station M3, midway to the shelf edge.

Numbers of the remaining aforementioned species, though variable, did not attain the high levels of abundance observed for *Calanus* spp.. Numbers of *Pseudocalanus* spp. (Figure 4.20d) were relatively high (>$10^3 m^{-3}$) at stations in the North Channel, at the entrance to the Clyde and on the Malin Shelf. Lower numbers (<$500m^{-3}$) were recorded at stations in the inner Firths of Clyde and Lorn. Numbers of *A. clausi* were variable, but did not exceed $5x10^3 m^{-3}$ (Figure 4.20e). Areas of peak abundance were located in Loch Fyne, the North Channel and in the outer Firth of Lorn. High abundances of *Oithona* spp. occurred in the North Channel and at station FL0 on the Malin Shelf with lower numbers collected in the Firths of Lorn and Clyde (Figure 4.20g). *O. similis*

Figure 4.20 Distribution of 'common' species collected at stations sampled at 30m in May 1986. The full range of values used in this figure is shown below.





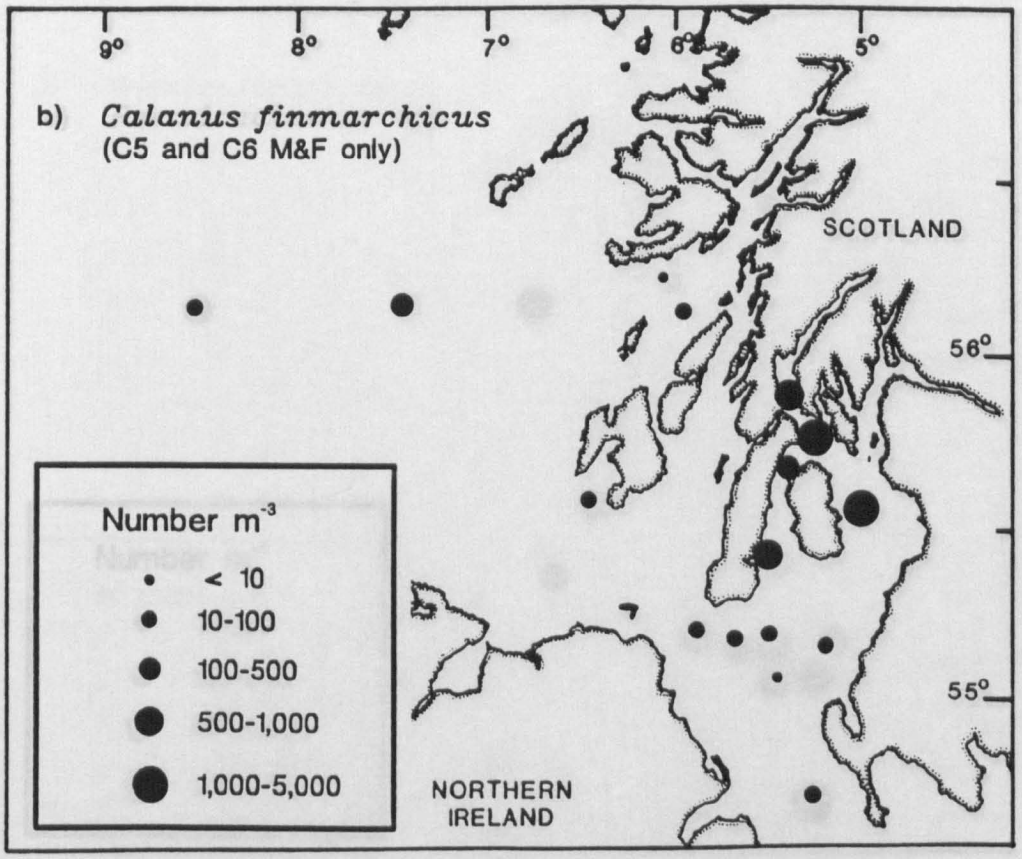
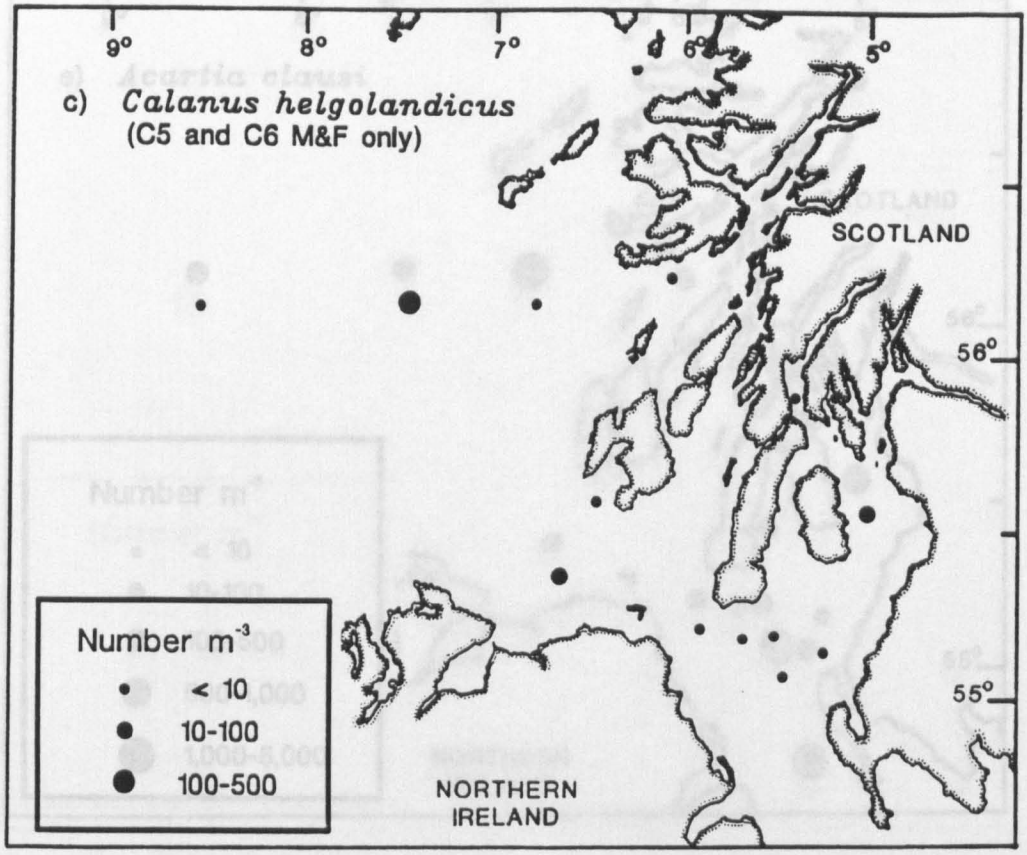


Figure 4.20 (Continued). Distribution of *Calanus* spp. (a) and *Calanus finmarchicus*, stages C5 and C6 only, (b) collected at 30m in May 1986.



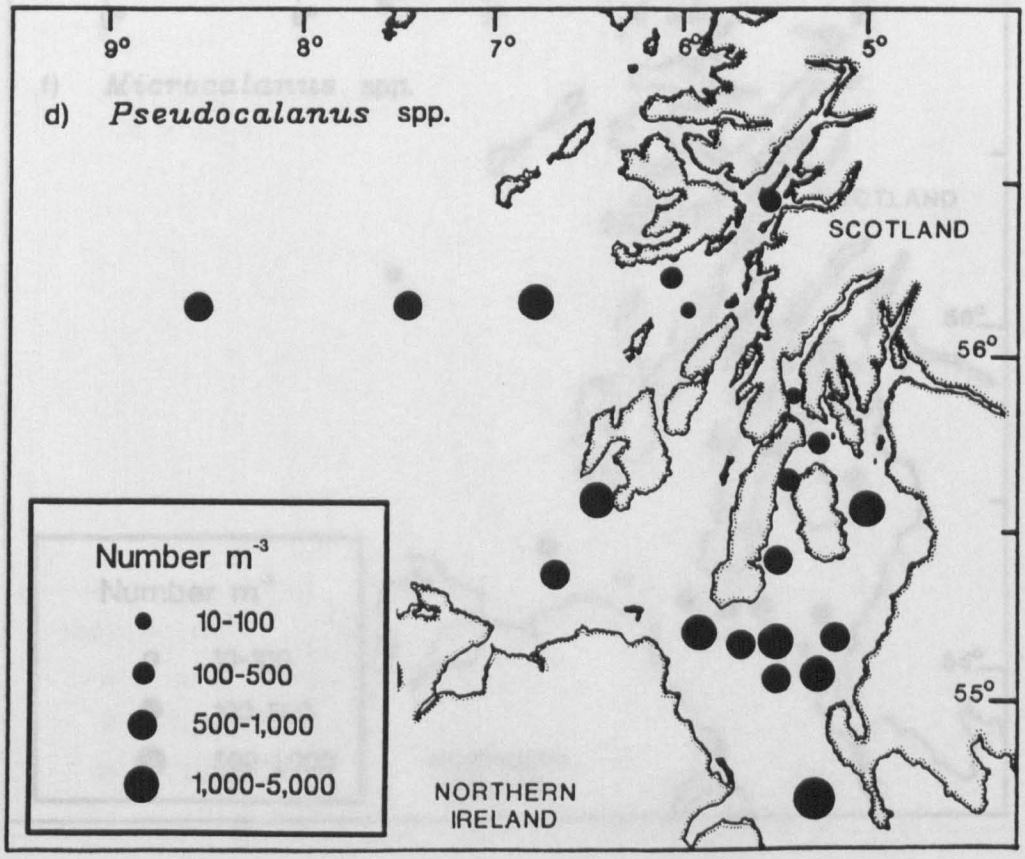
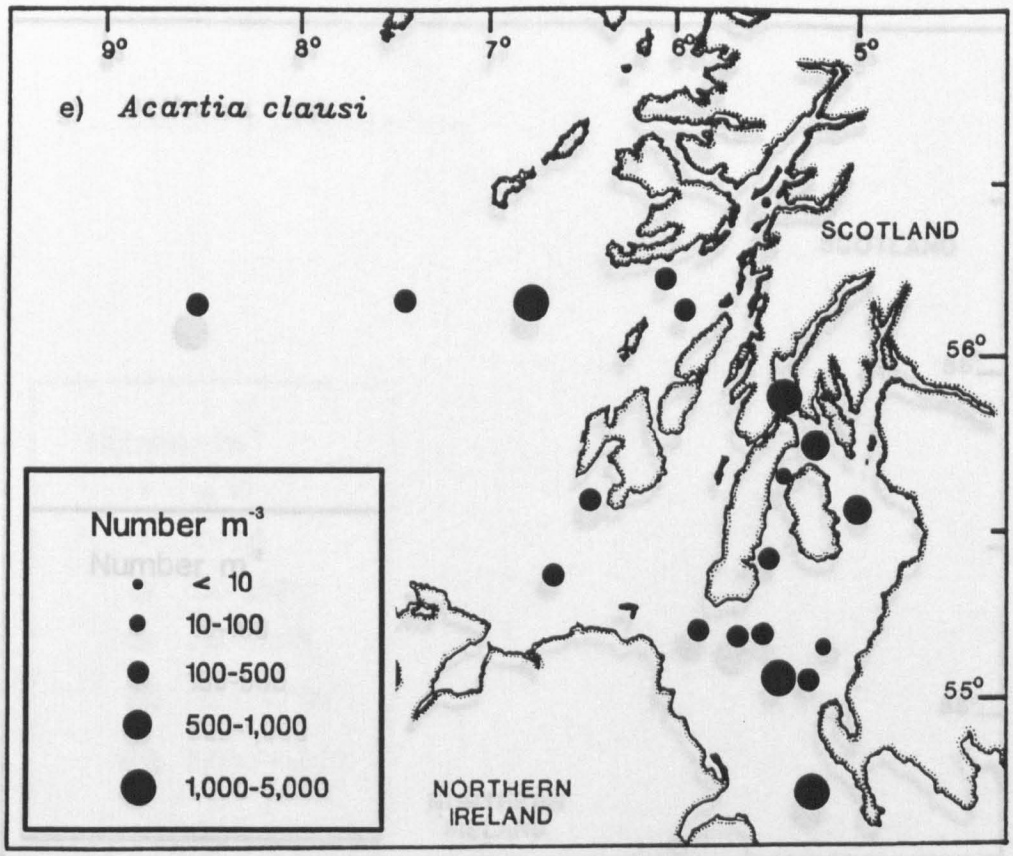


Figure 4.20 (Continued). Distribution of *Calanus helgolandicus*, stages C5 and C6 only, (c) and *Pseudocalanus* spp. (d) collected at 30m in May 1986.



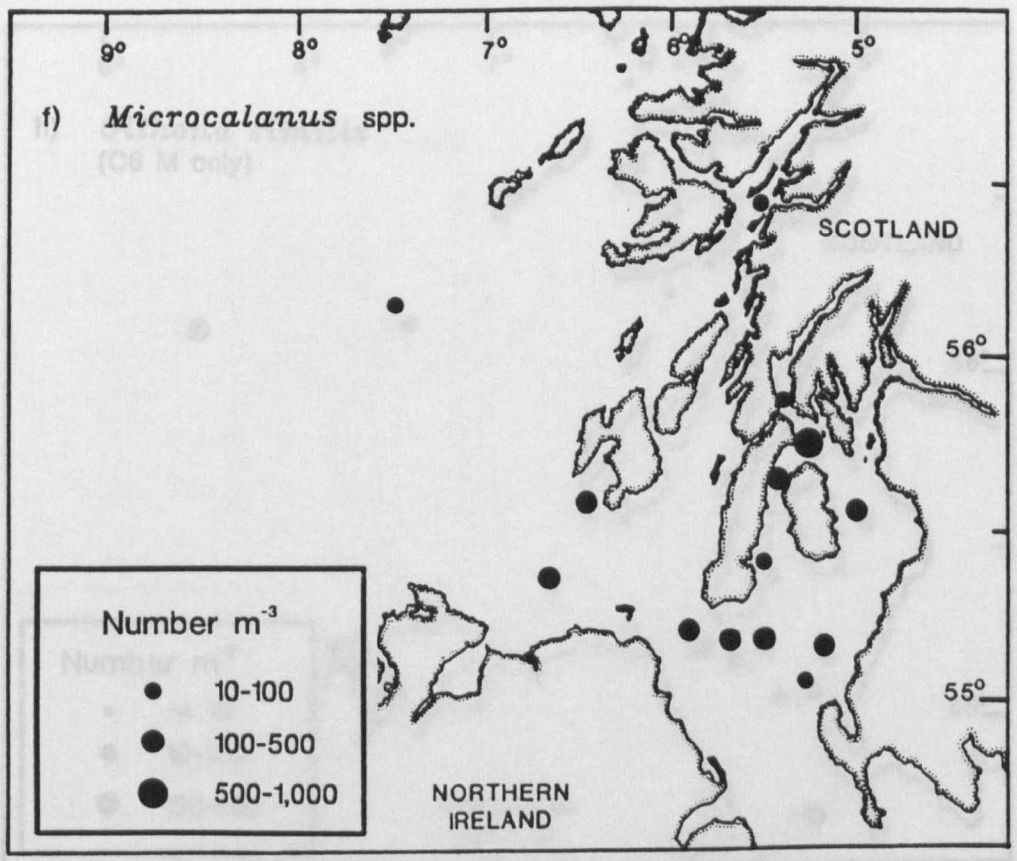
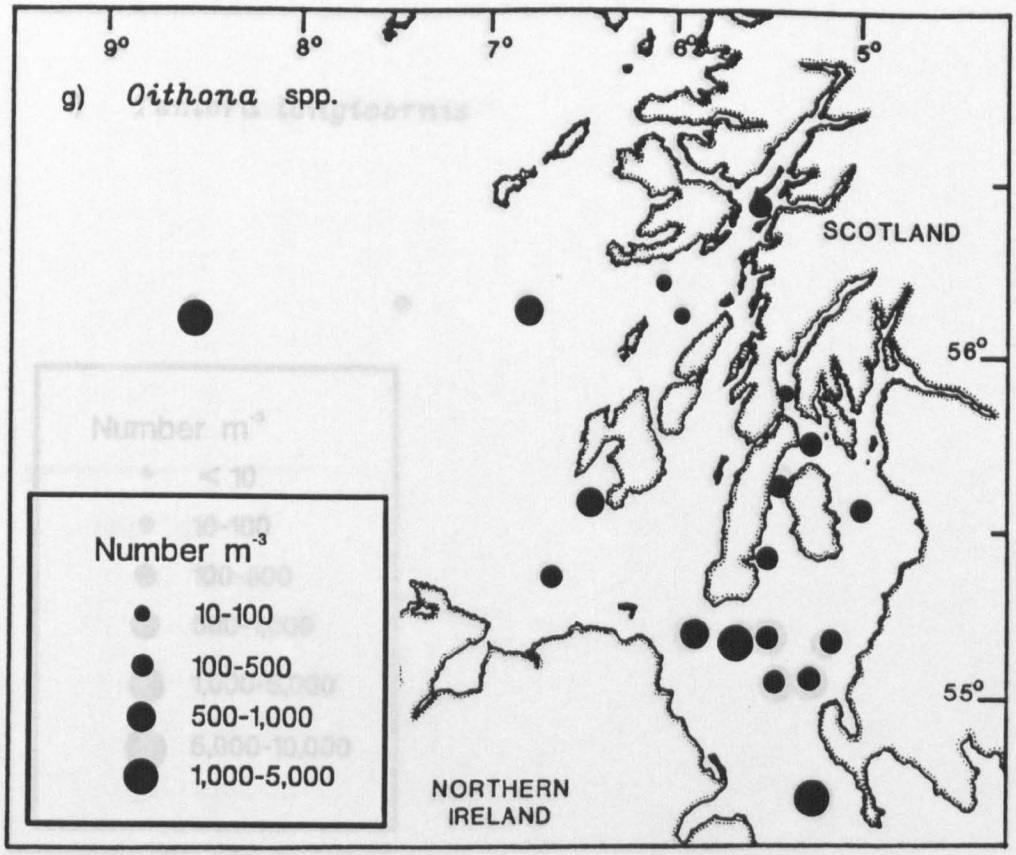


Figure 4.20 (Continued). Distribution of *Acartia clausi* (e) and *Microcalanus* spp. (f) collected at 30m in May 1986.



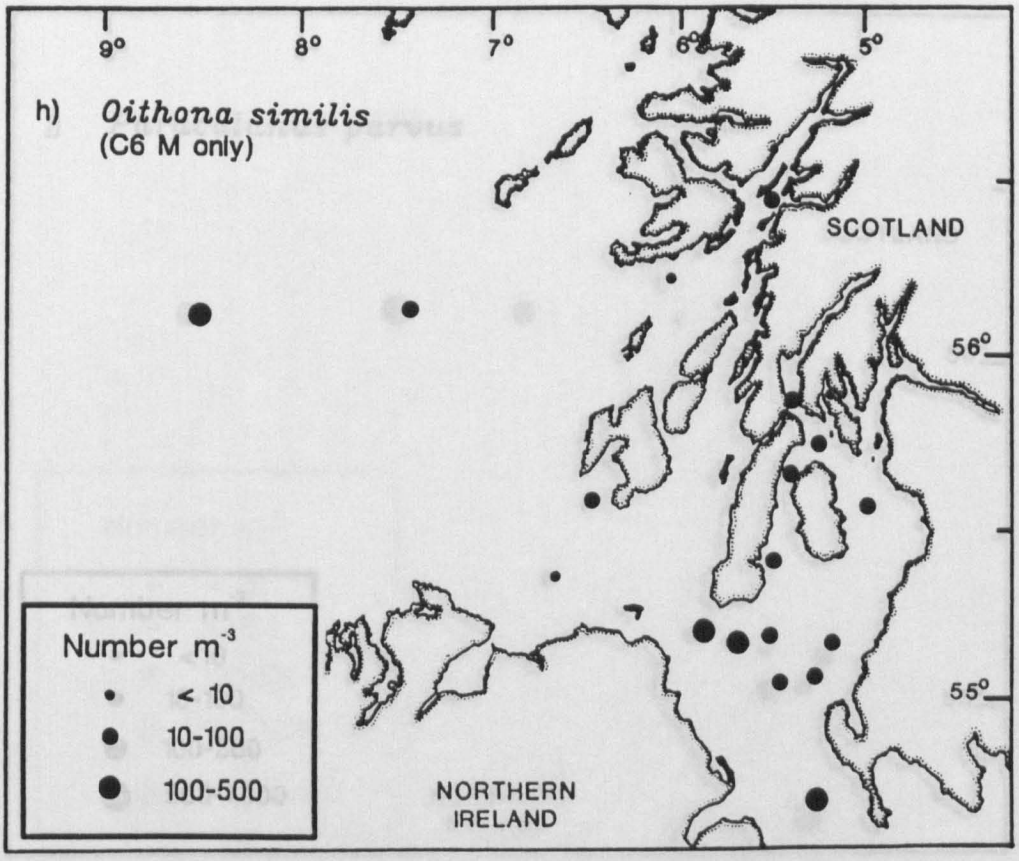
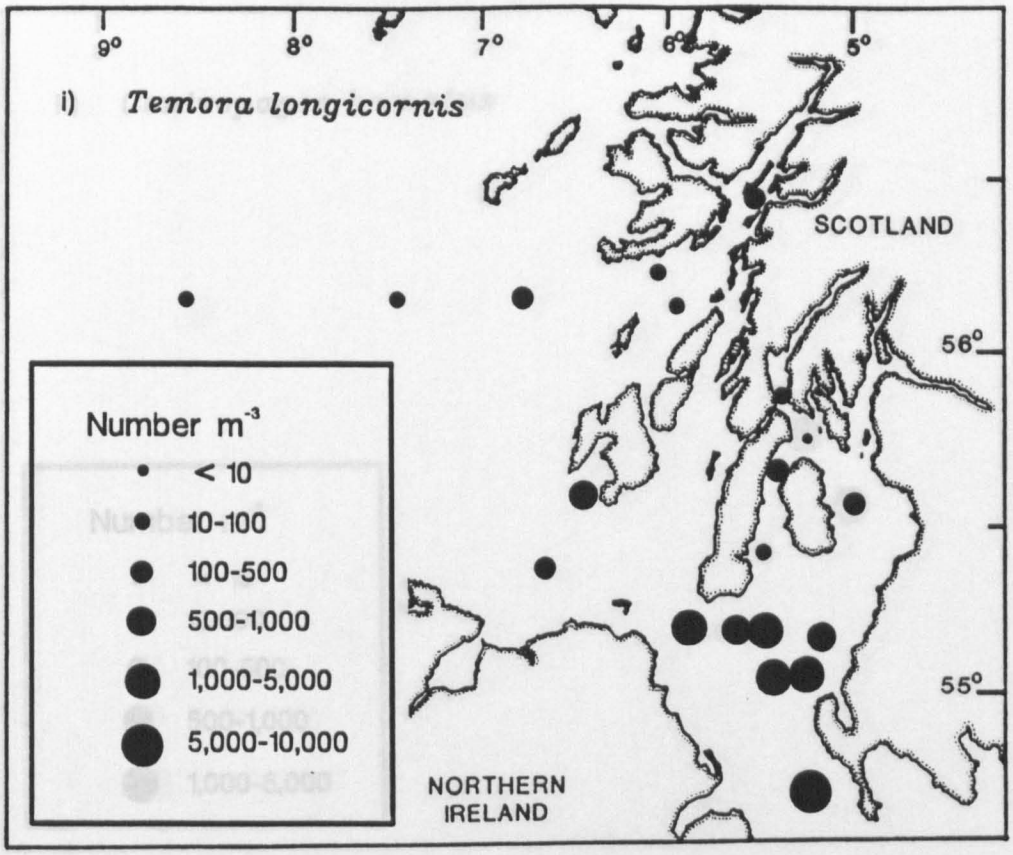


Figure 4.20 (Continued). Distribution of *Oithona* spp. (g) and *Oithona similis*, C6 males only, (h) collected at 30m in May 1986.



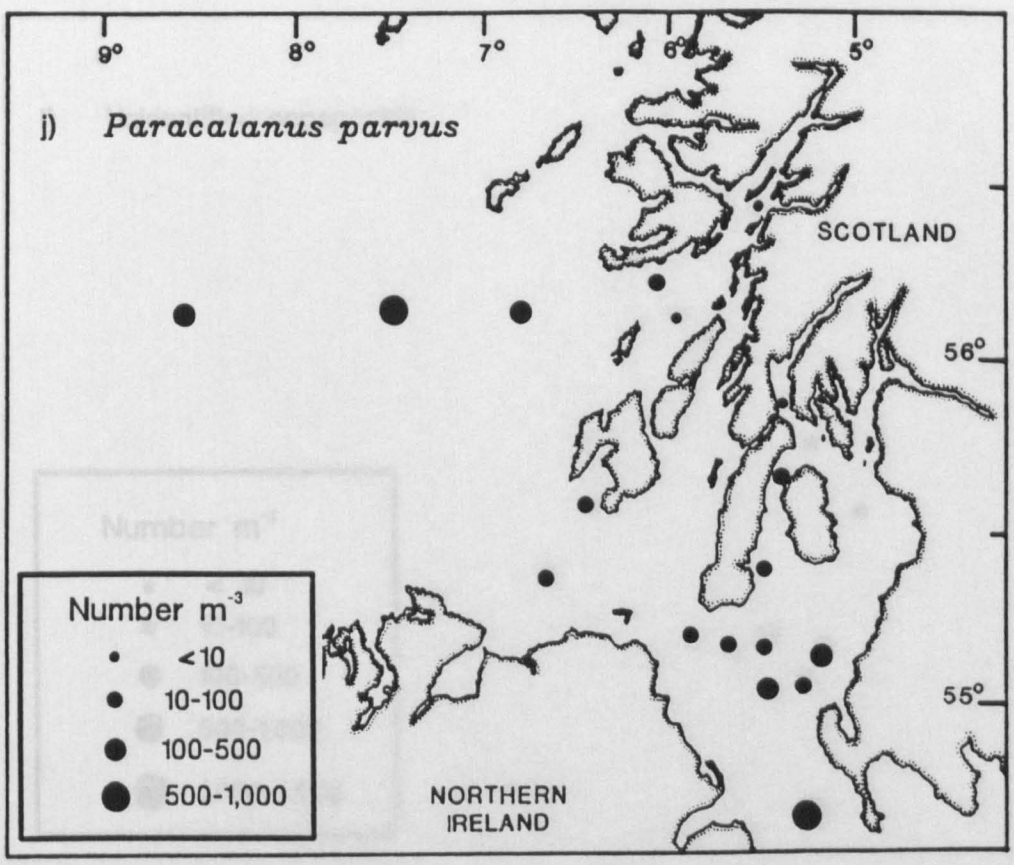
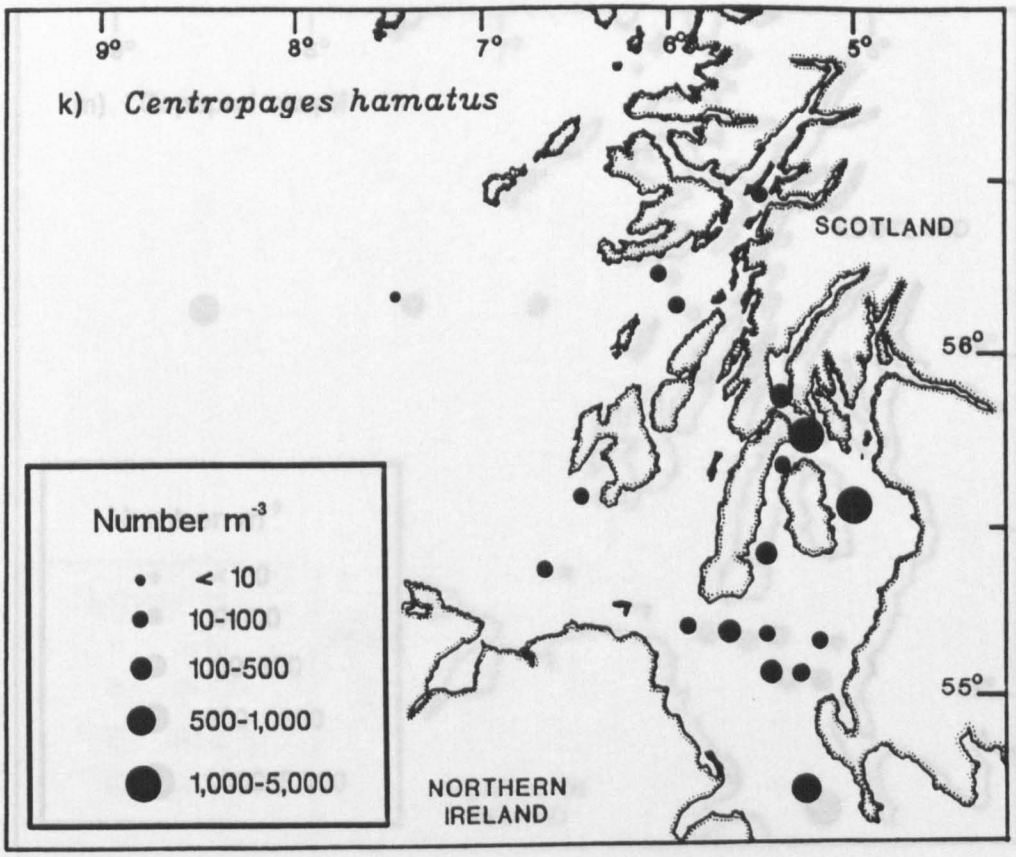


Figure 4.20 (Continued). Distribution of *Temora longicornis* (i) and *Paracalanus parvus* (j) collected at 30m in May 1986.



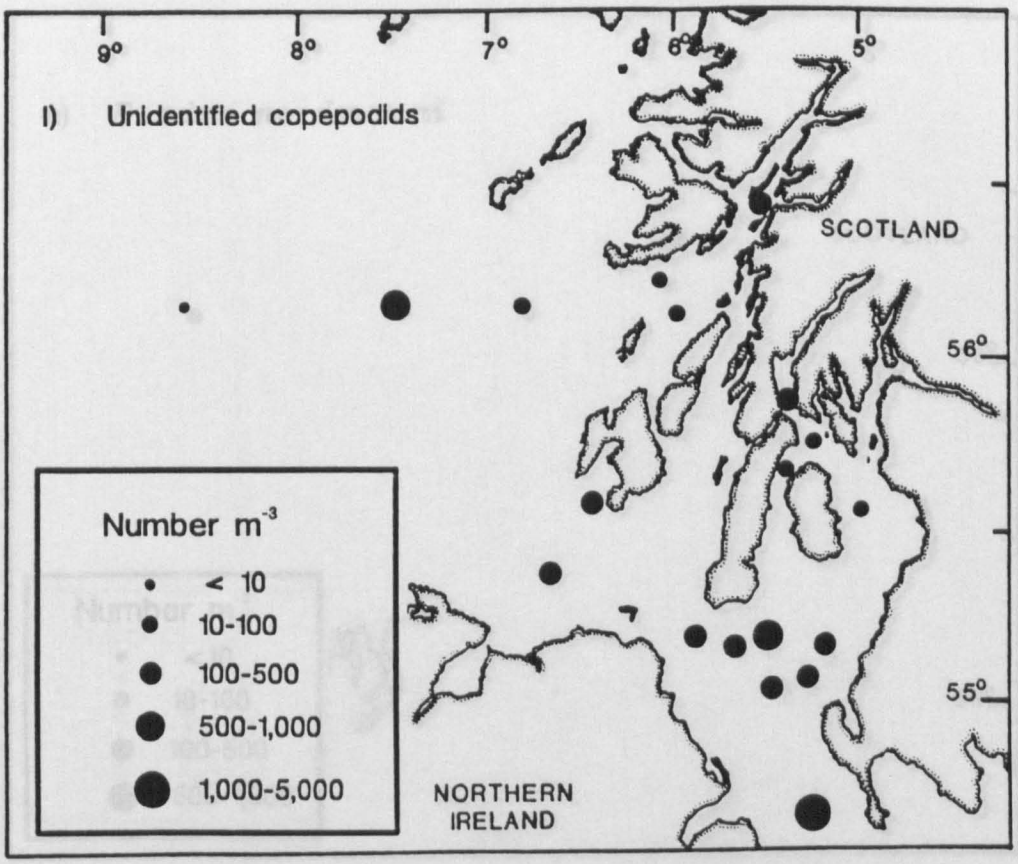
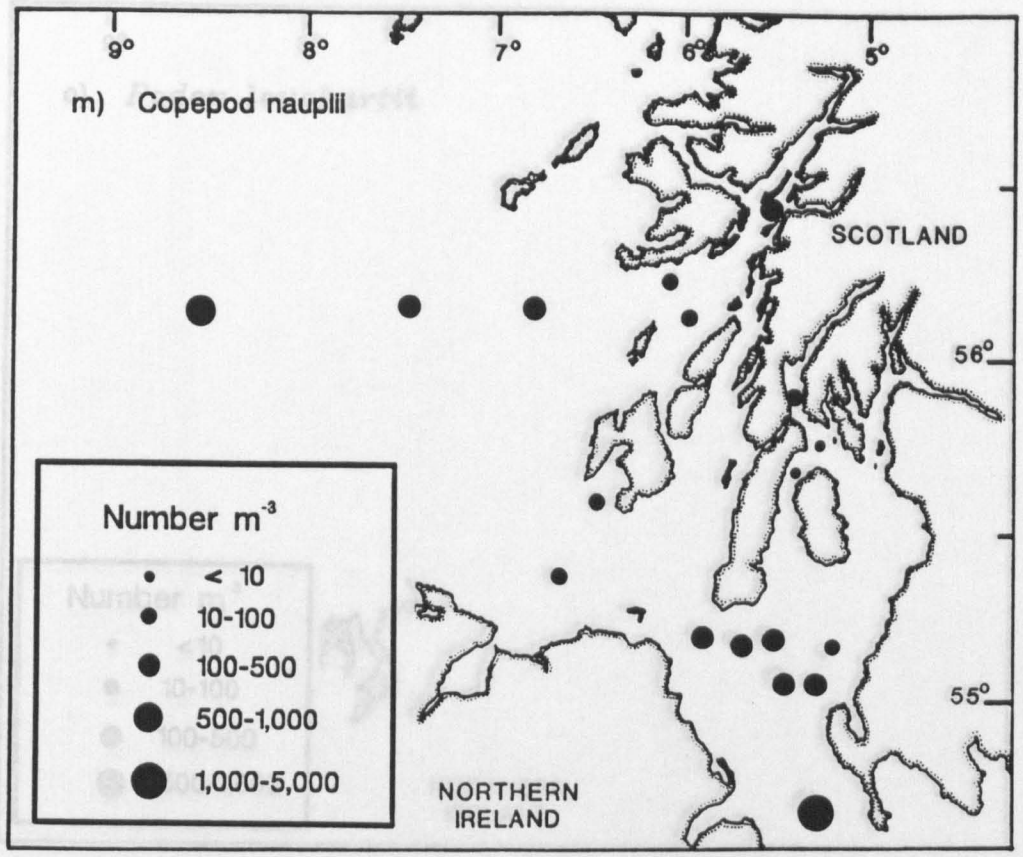


Figure 4.20 (Continued). Distribution of *Centropages hamatus* (k) and unidentified copepodids (l) collected at 30m in May 1986.



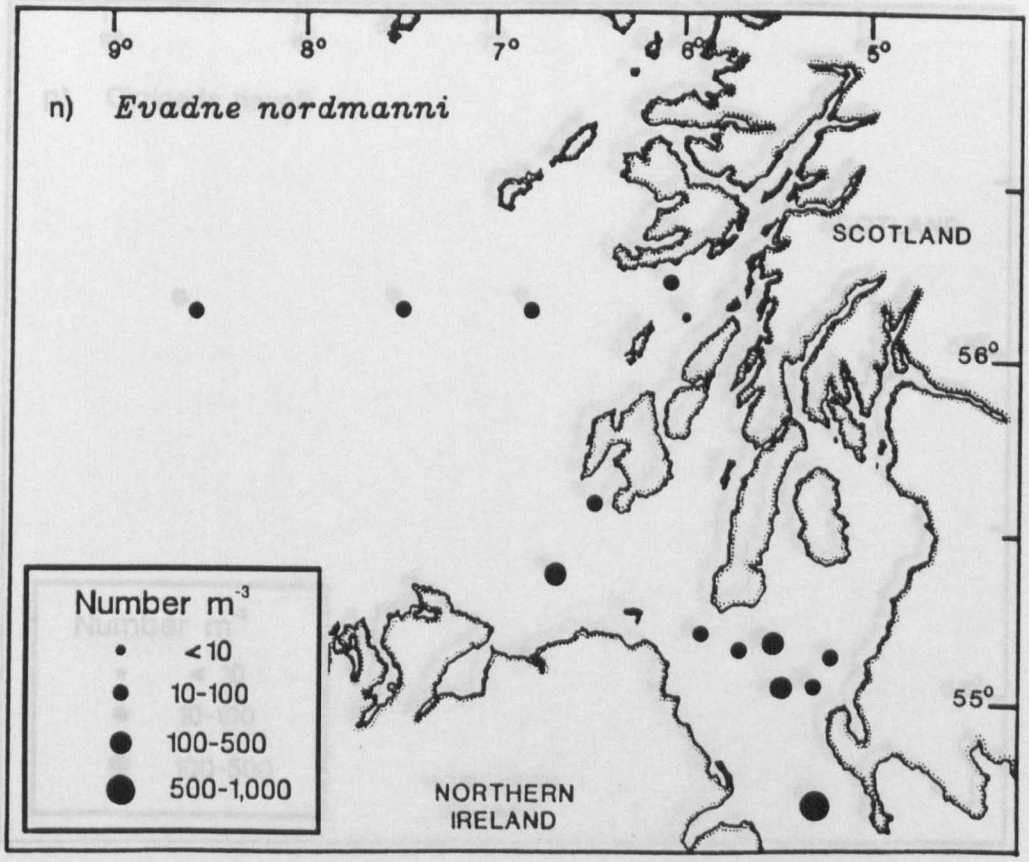
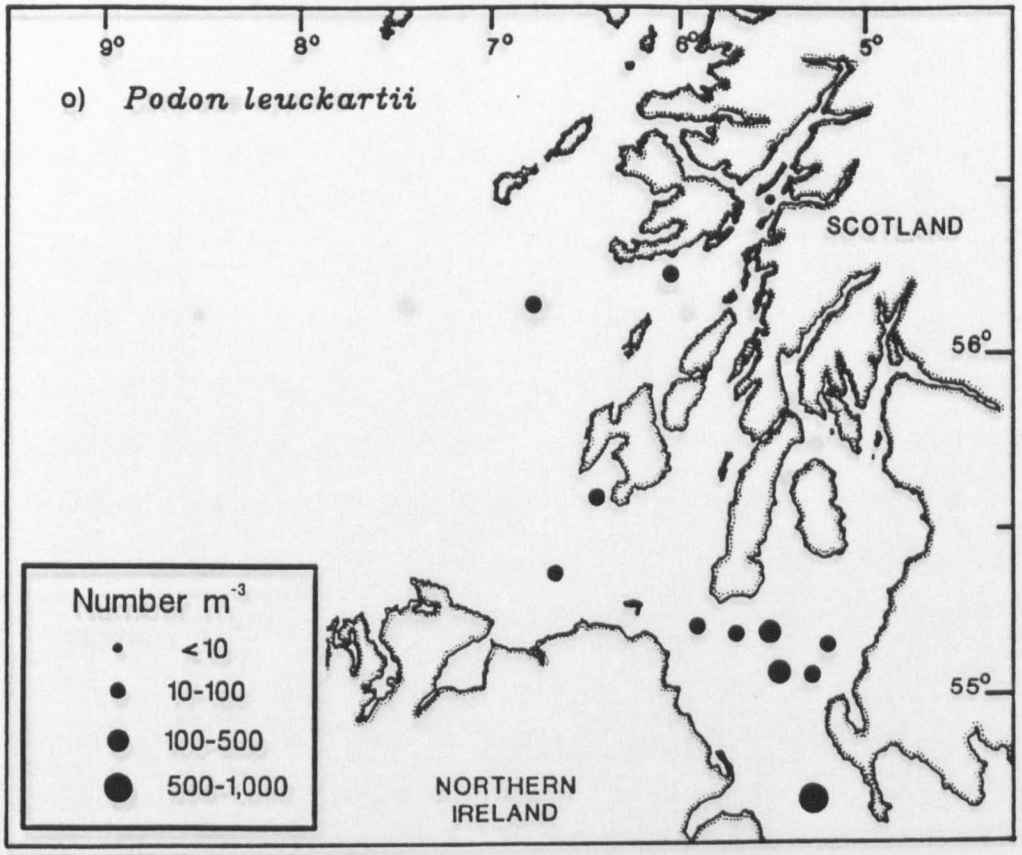


Figure 4.20 (Continued). Distribution of copepod nauplii (m) and *Evadne nordmanni* (n) collected at 30m in May 1986.



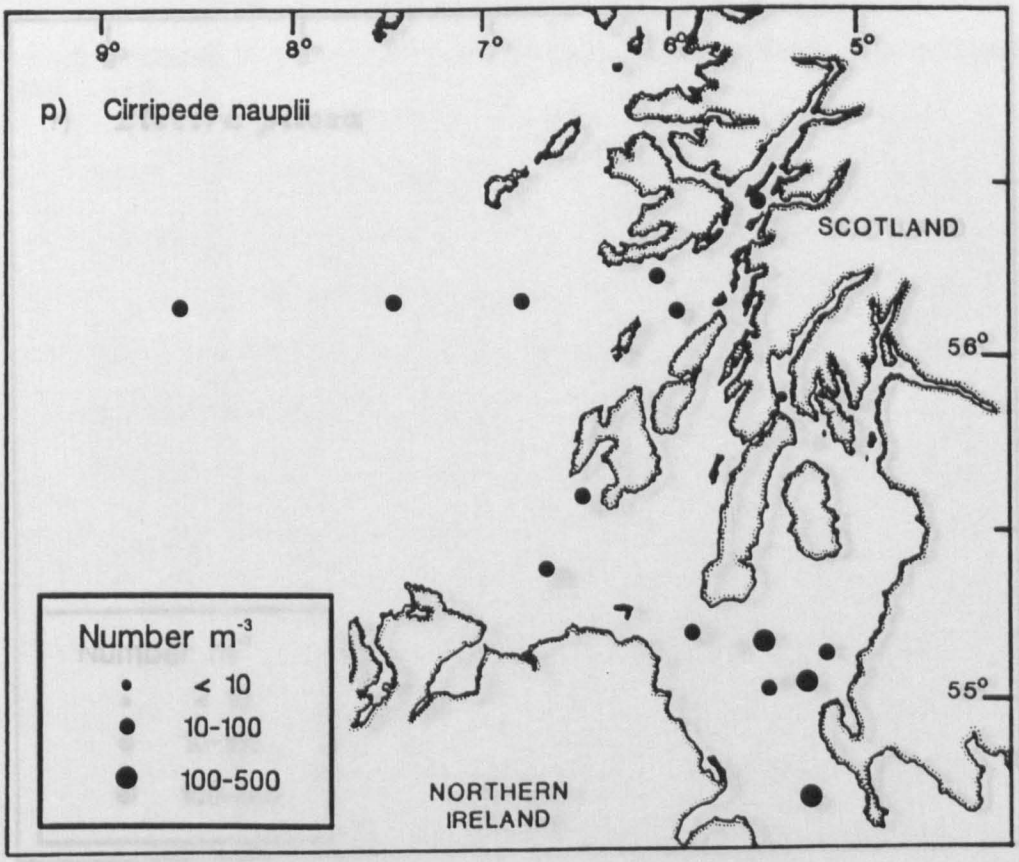
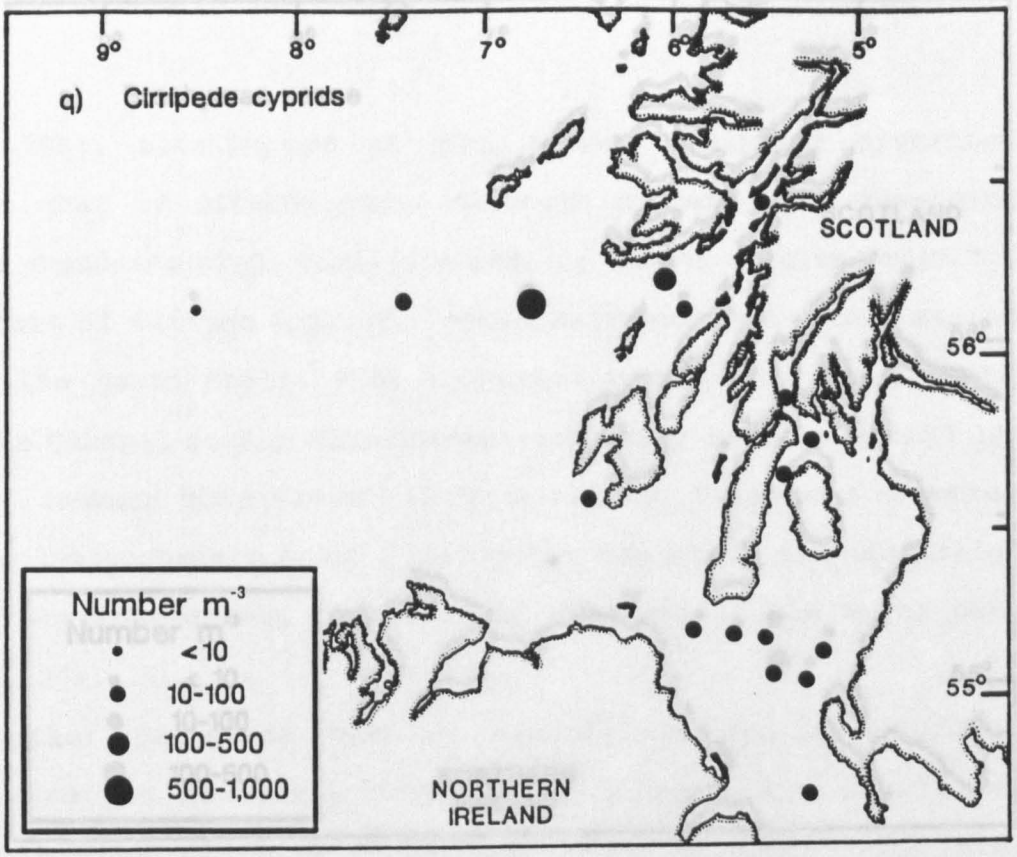


Figure 4.20 (Continued). Distribution of *Podon leuckartii* (o) and cirripede nauplii (p) collected at 30m in May 1986.



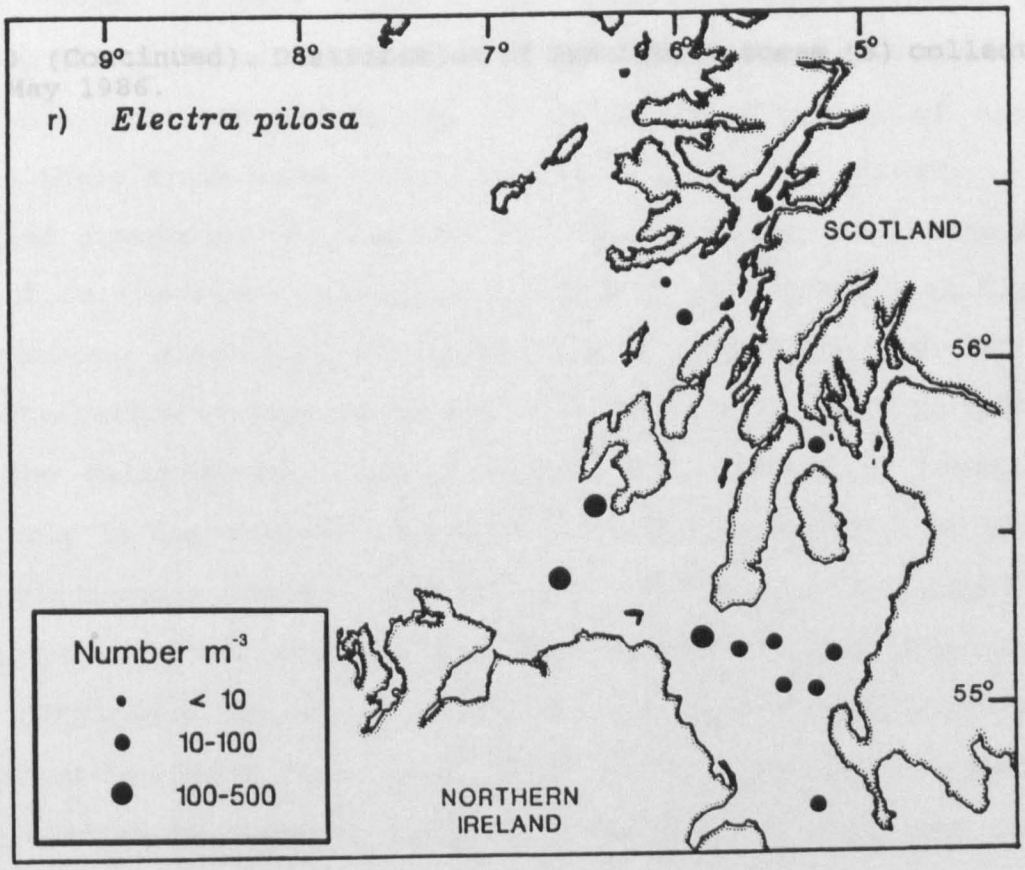


Figure 4.20 (Continued). Distribution of cirripede cyprids (q) and *Electra pilosa* (r) collected at 30m in May 1986.

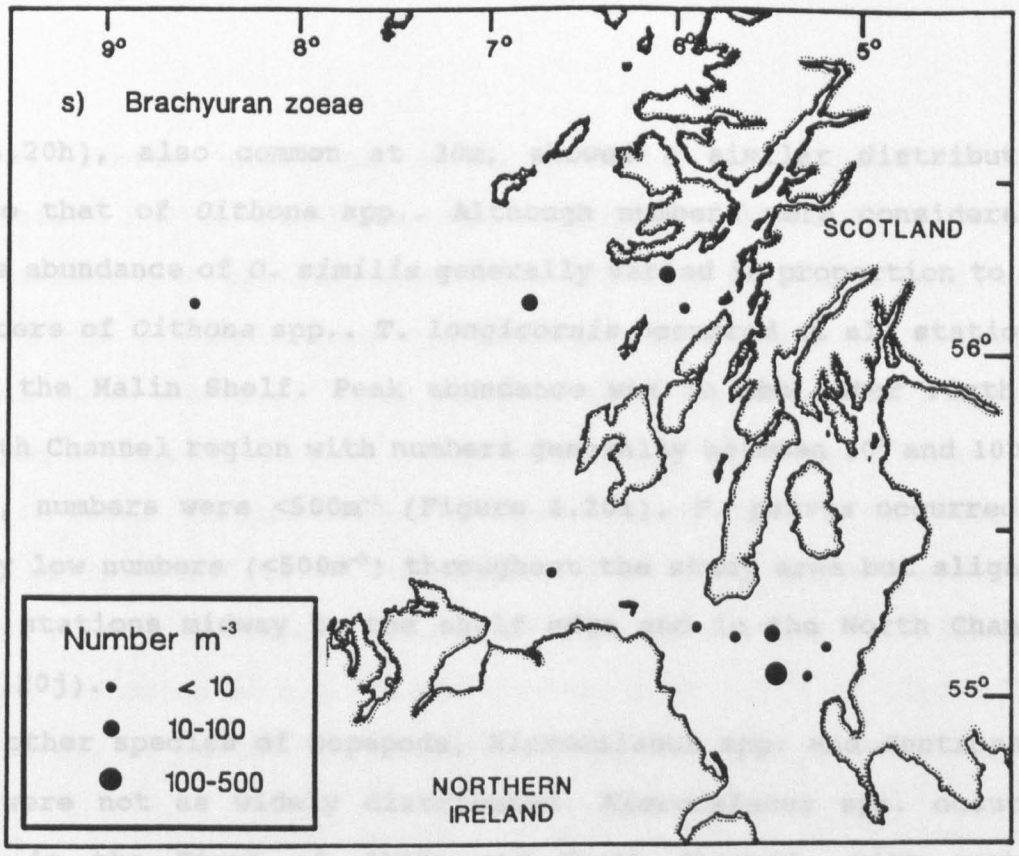


Figure 4.20 (Continued). Distribution of Brachyuran zoeae (s) collected at 30m in May 1986.

(Figure 4.20h), also common at 30m, showed a similar distribution pattern to that of *Oithona* spp.. Although numbers were considerably lower, the abundance of *O. similis* generally varied in proportion to the total numbers of *Oithona* spp.. *T. longicornis* occurred at all stations, including the Malin Shelf. Peak abundance was in the outer Firth of Clyde/North Channel region with numbers generally between 10^3 and $10^4 m^{-3}$. Elsewhere, numbers were $<500 m^{-3}$ (Figure 4.20i). *P. parvus* occurred in relatively low numbers ($<500 m^{-3}$) throughout the study area but slightly higher at stations midway to the shelf edge and in the North Channel (Figure 4.20j).

Two other species of copepods, *Microcalanus* spp. and *Centropages hamatus*, were not as widely distributed. *Microcalanus* spp. occurred primarily in the Firth of Clyde and North Channel, with numbers generally $<500 m^{-3}$ (Figure 4.20f). *C. hamatus* (Figure 4.20k) was distributed primarily in the Firths of Lorn and Clyde and in the North Channel, with greatest abundances to the north and east of Arran. Numbers in these areas were $>10^3 m^{-3}$, elsewhere generally $<500 m^{-3}$. Unidentified copepodids (Figure 4.20l), although widespread, were most predominant in the North Channel and entrance to the Firth of Clyde, with high numbers also on the Malin Shelf. This pattern was also evident in the distribution of copepod nauplii (Figure 4.20m) with high numbers also on the Malin Shelf. Copepod nauplii were generally absent or occurred only in low numbers at stations in the inner Firth of Clyde.

The cladocerans, *Evadne nordmanni* and *Podon leuckartii*, were found in all regions of the study area with the exception of the inner Firth of Clyde (Figures 4.20n and o). This distribution virtually mirrored that observed for these species at 10m (Figures 4.19l and m). Numbers for both species were relatively low in comparison with the common copepods and did not exceed 10^3 individuals m^{-3}.

Finally, four meroplanktonic forms were also common in the fauna. Cirripede nauplii and cyprids were collected at all stations sampled

along the FL transect extending from station FL15 in the inner Firth of Lorn to station FL0 on the Malin Shelf (Figures 4.20p and q). Nauplii were less common than cyprids, the latter having a peak in abundance in the outer Firth of Lorn. Both occurred in low numbers in the North Channel and outer Firth of Clyde, and in Loch Fyne, but only cyprids were collected from Kilbrannan Sound. Brachyuran zoeae were also found on the Malin Shelf (Figure 4.20s) in low numbers ($<10m^{-3}$) although the main areas of distribution were in the Firth of Lorn, North Channel and outer Firth of Clyde. *Electra pilosa* exhibited a similar distribution, in addition occurring at one station in the inner Firth of Clyde. Once again, however, *E. pilosa* was not found west of 7°W (Figure 4.20r).

4.2.3 Multivariate Analyses

In the following sections the results of multivariate cluster and ordination analyses are presented. In all cases, clusters were chosen in order to obtain the best groupings for the dendrogram and ordination plots combined. Similarity levels used to identify clusters on the dendrogram were subsequently superimposed onto the ordination plot to demarcate station or species groups. All main station groups were delineated using a solid line while subgroups were delineated using a broken line. Since MDS compares similarities only in terms of their rank order, there is no scale included on the ordination plots. Plot orientation is also arbitrary as only relative distances among entities (i.e. station or species groups) are meaningful. Stress levels quoted for all MDS analyses refer to the two-dimensional stress, unless otherwise stated. In cases where three-dimensional MDS configuration solutions are given, it should be noted that these are for comparative purposes and that all subsequent analyses are based on the two-dimensional results. Station locations corresponding to sample numbers used in the dendrogram and ordination plots are given in Table 4.7.

Table 4.7 Station locations corresponding to numbers used in the cluster dendrograms and ordination plots for the March 1987 and May 1986 cruises. N and D are used to denote night and day collections made at the same stations.

Number	March 1987	May 1986
1	FL15	FL15
2	FL13	FL12(N)
3	FL12	FL12(D)
4	FL9	FL8*
5	FL0	M3
6	D0	FL1
7	D4	E2
8	D7	Z4
9	C3	Y3(D)
10	C5	Y3(N)
11	A4	Y5
12	A2	A3
13	Z4	C6
14	Y1	C3
15	Y3	AB30
16	AB3A	AB8
17	AB5	AB3A
18	AB8	AB5
19	AB1**	AB17
20	AB17	AB44
21	AB15	AB38
22	AB14	AB40
23	AB20	
24	AB25	
25	AB28	
26	AB22	
27	AB30	
28	AB34	
29	AB35A	
30	AB38A	
31	AB38	
32	AB40	
33	AB44	

* not sampled at 10m
** not sampled at 30m

4.2.3.1 March 1987: 10m

4.2.3.1.1 Station Analysis

The cluster analysis for samples collected at 10m in March 1987 revealed five station groups at a level of 60% similarity (Figure

4.21a). Three of these groups could be associated with a given region of the study area: 'OL', the outer Firth of Lorn; 'IL', the inner Firth of Lorn; 'MS', the Malin Shelf. Although the two remaining groups, designated 'FC' and 'NC', contained only stations located in the Firth of Clyde and North Channel, the spatial relationship among stations within groups and subgroups was not well-defined. Four subgroups were identified within the Firth of Clyde. Subgroup FC4 contained three stations located in the vicinity of Loch Striven, while subgroup FC2 contained stations located in the outer Firth of Clyde to the south and south-east of Arran. The remaining subgroups, FC1 and FC3, and group NC contained a mixture of stations from both the Firth of Clyde and North Channel. A map of the study area showing the location of stations within each of the clusters is given in Figure 4.22.

Ordination plots of both the two- and three-dimensional MDS solutions are given in Figures 4.21b and c. Stress levels were 0.17 and 0.11, respectively. The two-dimensional plot (Figure 4.21b) was in good agreement with the cluster results. Superimposing the 60% similarity level from the dendrogram onto the ordination plot again delineated the five station groups. Groups OL, IL, and MS representing the outer and inner Firth of Lorn and Malin Shelf, respectively, appeared quite distinct from groups FC and NC which contained Firth of Clyde and North Channel stations. The ordination plot clearly illustrated the complex nature of station clusters within the Firth of Clyde and suggested that some of the clusters may not have been as distinct as displayed by the dendrogram (e.g. groups FC1 and FC4).

Overall, station groupings in the three-dimensional plot (Figure 4.21c) did not differ markedly from those shown in the two-dimensional plot (Figure 4.21b). However, station AB40 which, based on the results of the corresponding cluster analysis, was included in the 'NC' group, clearly formed part of the 'FC' group (i.e. FC1 subgroup) in the three-dimensional solution. Given the considerable drop in stress levels

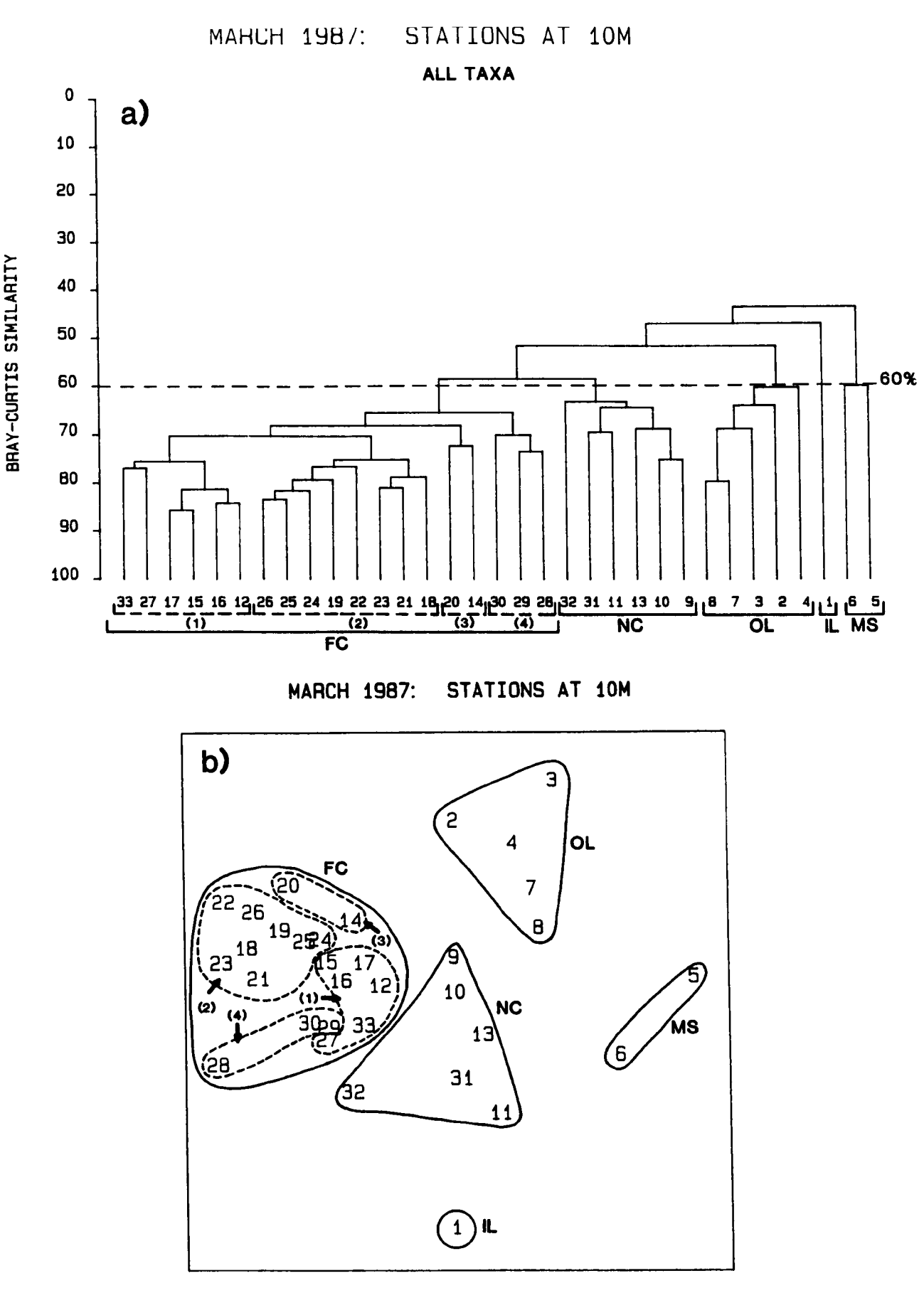


Figure 4.21 Cluster results (a) and two-dimensional MDS configuration solution (b) for analyses using all taxa collected at 10m in March 1987. FC = Firth of Clyde, NC = North Channel, OL = Outer Lorn, IL = Inner Lorn, MS = Malin Shelf.

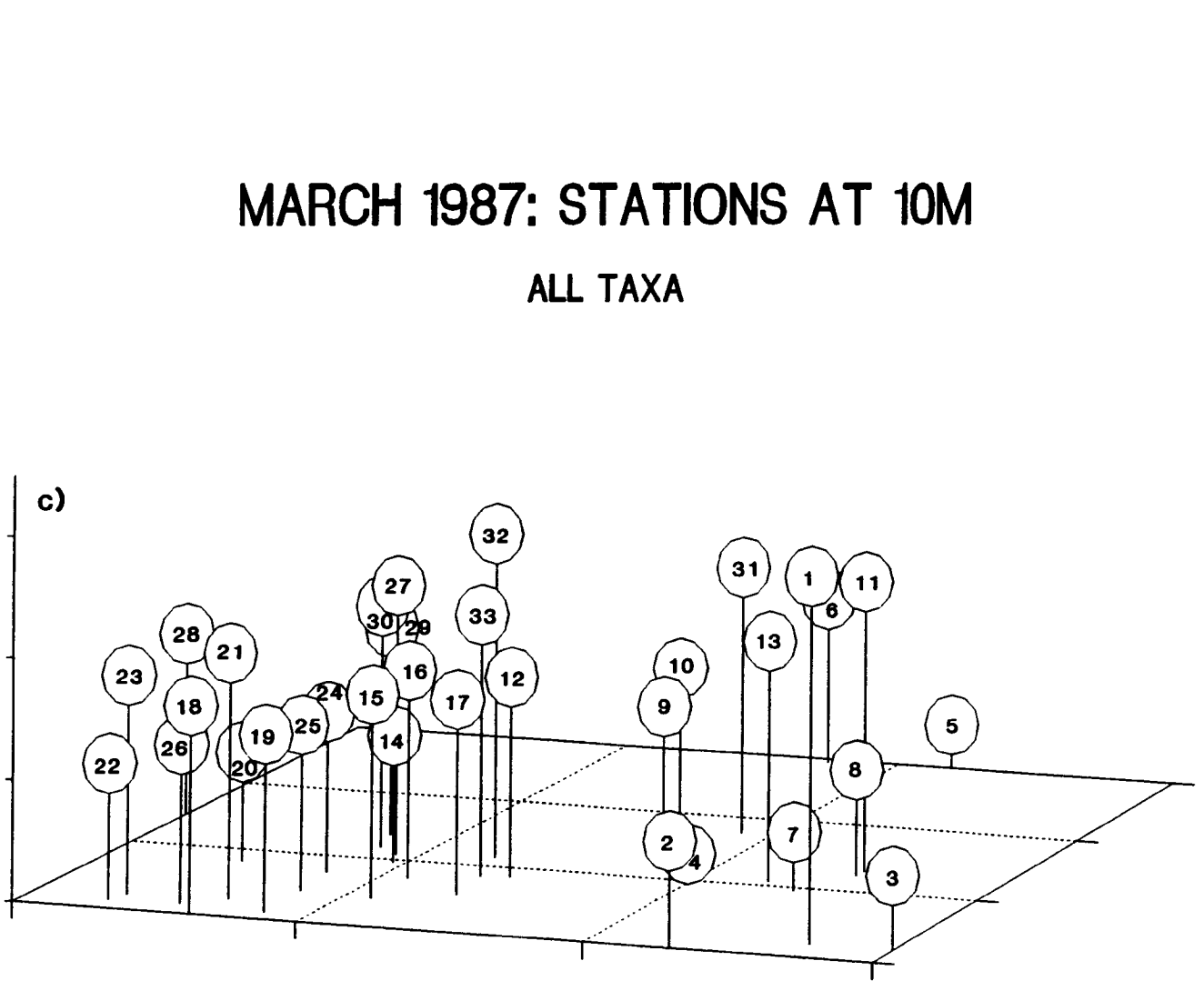


Figure 4.21 (Continued). Three-dimensional MDS configuration solution for analysis using all taxa collected at 10m in March 1987. Station numbers correspond with those listed in Table 4.7.

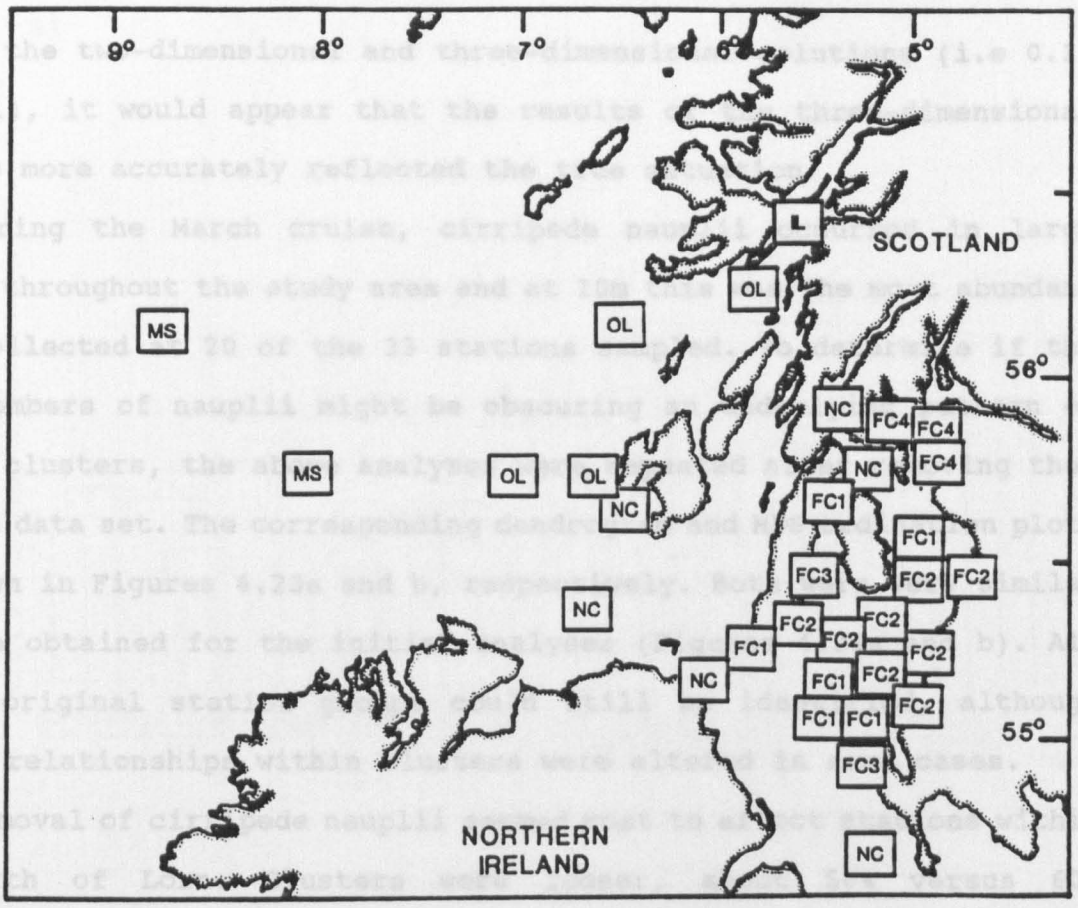


Figure 4.22 Location of station groups identified in cluster and two-dimensional MDS analyses using all taxa collected at 10m in March 1987. FC = Firth of Clyde, NC = North Channel, OL = Outer Lorn, IL = Inner Lorn, MS = Malin Shelf.

between the two-dimensional and three-dimensional solutions (i.e 0.17 and 0.11), it would appear that the results of the three-dimensional analysis more accurately reflected the true situation.

During the March cruise, cirripede nauplii occurred in large numbers throughout the study area and at 10m this was the most abundant taxon collected at 20 of the 33 stations sampled. To determine if the large numbers of nauplii might be obscuring an underlying pattern of station clusters, the above analyses were repeated after removing them from the data set. The corresponding dendrogram and MDS ordination plots are shown in Figures 4.23a and b, respectively. Both were very similar to those obtained for the initial analyses (Figures 4.21a and b). All of the original station groups could still be identified, although station relationships within clusters were altered in some cases.

Removal of cirripede nauplii seemed most to affect stations within the Firth of Lorn. Clusters were looser, about 50% versus 60% similarity, and station FL9 previously clustered with stations in the outer Firth of Lorn (group OL) now formed part of the Malin Shelf (MS) group. Within the Firth of Clyde and North Channel, the overall integrity of the station clusters was maintained. The only major alteration in station organisation was observed in subgroup FC4 which contained stations located in the inner Clyde. Two stations previously in this subgroup, AB35A and AB38A were now part of subgroup FC1. Subgroups FC2 and FC3 and group NC remained largely unaffected.

The MDS plot was again in good agreement with the dendrogram results regarding coarse-scale station relationships. The five station groups identified in the initial analysis showed a similar pattern of spatial separation on the ordination plot (Figure 4.23b). Within the Firth of Clyde group, station clusters appeared to be more orderly but relationships were still highly complex, particularly between groups FC1-FC3 which were all closely positioned on the ordination plot. A stress level of 0.17 was obtained for the analysis.

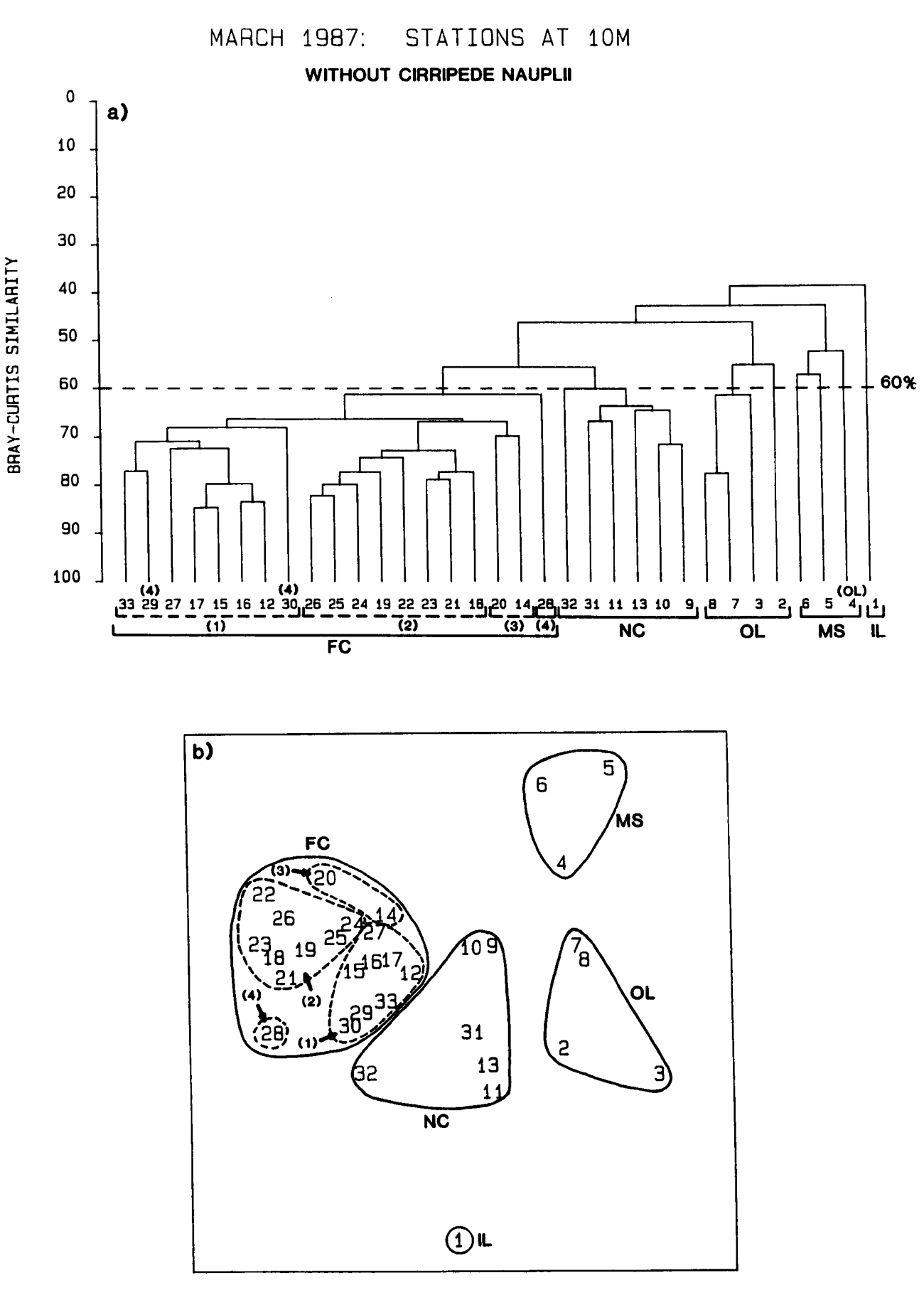


Figure 4.23 Cluster results (a) and two-dimensional MDS configuration solution (b) for analyses conducted excluding cirripede nauplii in March 1987 at 10m. Numbers enclosed in brackets (i.e. in (a)) indicate the station group in the original cluster analysis. FC = Firth of Clyde, NC = North Channel, OL = Outer Lorn, IL = Inner Lorn, MS = Malin Shelf.

4.2.3.1.2 Species Analysis

The results of the descriptive analysis showing the dominant faunas identified for station clusters at 10m in March are shown in Table 4.8. Faunal assemblages in all groups were composed of a small number of species and other taxa, most of which occurred in more than one group but in differing relative abundances (e.g. the relative positions of *Calanus* spp., cirripede nauplii and *Temora longicornis* throughout subgroups FC1 to FC4 in Table 4.8). One exception to this was cirripede nauplii which were abundant throughout the entire study area at this time. Other meroplanktonic forms such as polychaete larvae, cyphonautes of *Electra pilosa* and eggs of the gastropod *Littorina littorea*, were also common members of the fauna in several groups. On the larger scale, however, differences were apparent among the faunal assemblages. Compared with other regions, the fauna in the Firth of Clyde (i.e. subgroups FC1 to FC4) was largely dominated by *Calanus*, while that in the inner and outer Firth of Lorn (i.e. groups OL and IL) was quite depauperate with only meroplanktonic species occurring in any number. On the Malin Shelf (group MS), the fauna consisted primarily of a mixture of small copepods such as *Oithona* spp., *Paracalanus parvus*, and *Pseudocalanus* spp.. However, it is interesting to note that cirripede nauplii were also prominent at the shelf stations, ranking second in overall abundance. In the last remaining group, 'NC', which contained a mixture of stations in the North Channel and at the head of the Firth of Clyde, the fauna was primarily a mixture of small copepods such as *Oithona* spp. and meroplanktonic species, predominantly cirripede nauplii.

The results of the inverse analysis for March at 10m are shown in Figure 4.24. In order to derive the same number of species groups as station groups (Figures 4.21a and b) three clusters were identified at 30% similarity and two at 20% similarity (Figure 4.24a). The

Table 4.8 Rank order abundance of species and taxa in station clusters identified using multivariate analysis, for samples at 10m in March. Only species comprising ≥ 3% of the fauna are included. Labels for station clusters correspond to those in Figure 4.21. FC = Firth of Clyde; NC = North Channel; OL = Outer Lorn; IL = Inner Lorn; MS = Malin Shelf.

FC1	**FC2**	**FC3**	**FC4**
Cirripede nauplii	*Calanus* spp.	*Calanus* spp.	Cirripede nauplii
Calanus spp.	Cirripede nauplii	*Temora longicornis*	*Temora longicornis*
Temora longicornis	*Acartia clausi*	Cirripede nauplii	*Oithona* spp.
Acartia clausi	*Temora longicornis*	*Acartia clausi*	*Calanus* spp.
Microcalanus spp.	*Centropages hamatus*	*Pseudocalanus* spp.	
Oithona spp.		*Oithona* spp.	
Electra pilosa		*Electra pilosa*	
Polychaete larvae			

NC	**OL**	**IL**	**MS**
Cirripede nauplii	Cirripede nauplii	Cirripede nauplii	*Oithona* spp.
Oithona spp.	*Electra pilosa*	*Electra pilosa*	Cirripede nauplii
Temora longicornis		*Littorina littorea*	*Paracalanus parvus*
Acartia clausi			*Pseudocalanus* spp.
Microcalanus spp.			*Calanus* spp.
Calanus spp.			
Polychaete larvae			
Electra pilosa			

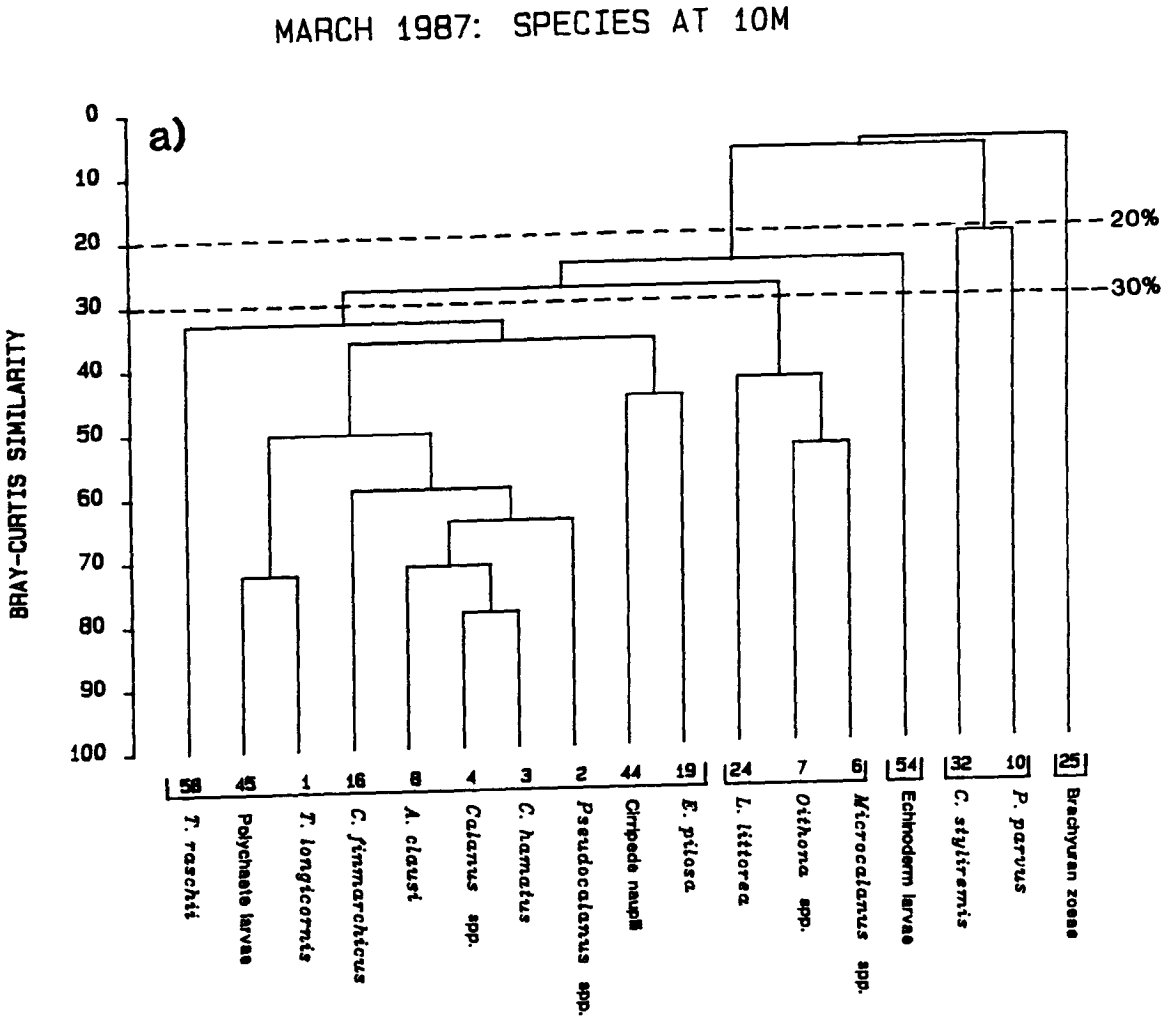


Figure 4.24 Species, or inverse, analysis results for March 1987 at 10m.

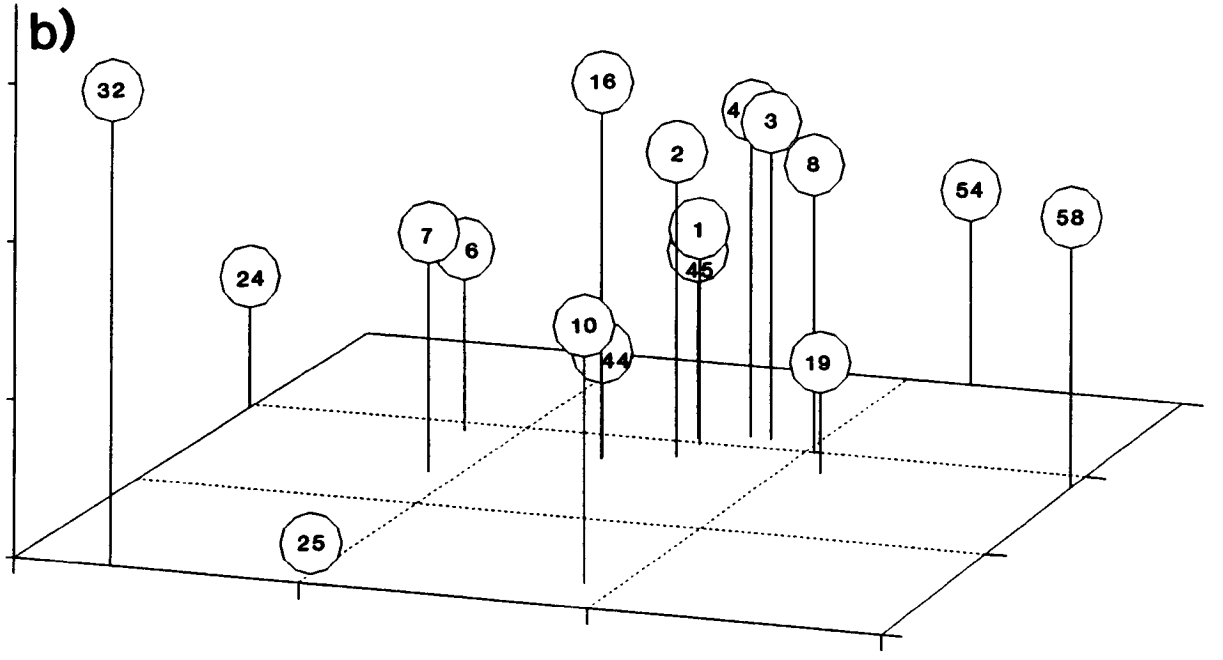


Figure 4.24 (Continued). Three-dimensional MDS configuration solution for species analysis at 10m in March 1987. Numbers correspond with the list of species shown in Figure 4.24a.

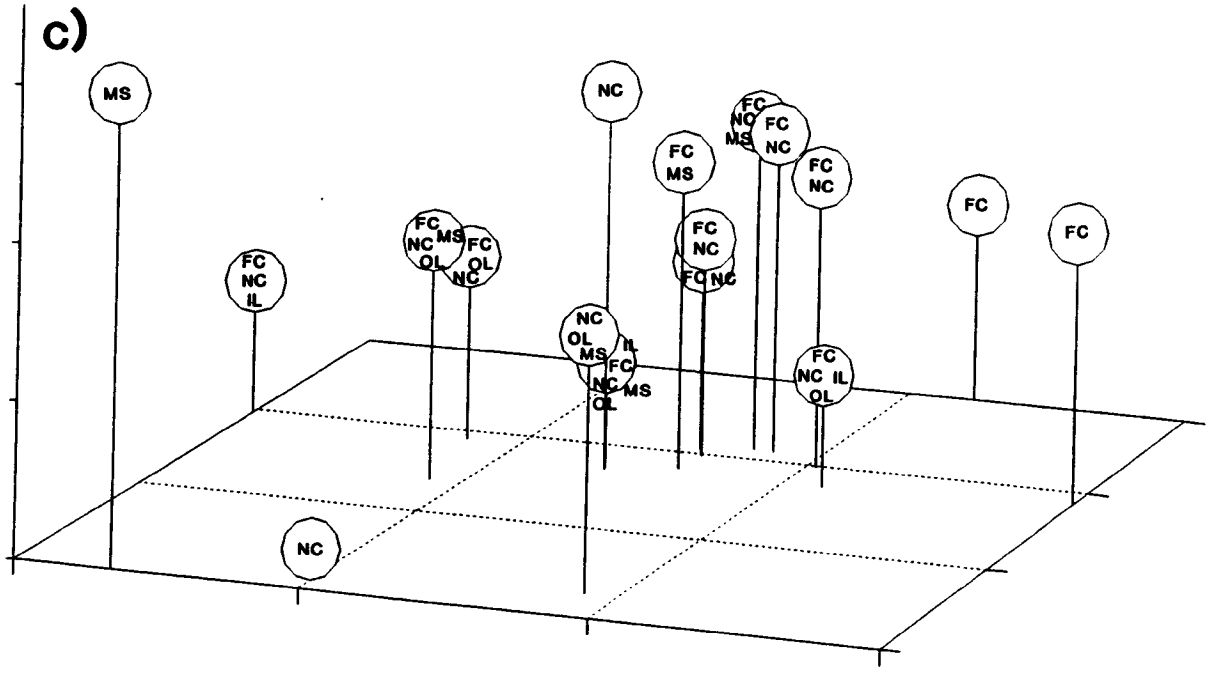


Figure 4.24 (Continued). Three-dimensional MDS configuration solution with species numbers replaced by the station group where the species or taxon accounted for >3% of the fauna at at least one station within the specified group. FC = Firth of Clyde, NC = North Channel, OL = Outer Lorn, IL = Inner Lorn, MS = Malin Shelf.

corresponding three-dimensional MDS plot with a stress of 0.07 is shown in Figure 4.24b. Figure 4.24c shows the same plot with species numbers replaced to show those station groups in which a given species or other taxon accounted for >3% of the fauna at at least one station within the specified group.

Of the 17 species or other taxa identified by the inverse analysis, only five occurred in a single station group. Four of these, *Calocalanus styliremis* Giesbrecht, *Calanus finmarchicus*, echinoderm larvae and brachyuran zoeae, occurred at only one station while *Thysanoessa raschii* occurred at just two stations. All five occurred at relatively low abundances, barely exceeding the 3% cut-off limit. The remaining 12 species or other taxa all occurred in more than one group, all five in the case of cirripede nauplii. As a result, when species positions on the ordination plot were replaced with the corresponding station labels, no clear pattern emerged regarding the importance of individual species in determining the station groupings. If subgroups are taken into account, the picture becomes even less clear.

Of the 17 species or other taxa identified as characterising the fauna using inverse analysis, 12 were also found to be characteristic of the fauna using the descriptive method. The latter also provided additional information regarding the relative importance of taxa within a group through rank ordering. The five taxa omitted from the descriptive analysis are those listed above. All occurred in relatively low abundances and at few stations. It is therefore unlikely that these taxa affected the initial station groupings although they may be of value as potential 'indicator' species for certain regions and therefore merit mention. In the case of the above species, *C. styliremis* appeared to be restricted to the offshore waters of the Malin Shelf while *T. raschii* was found mainly in the outer Firth of Clyde. The other three are probably of limited value as indicator species.

In the present study, the results of the inverse analysis were

generally not instructive and overall did not provide any additional information to that obtained using the descriptive technique. Although inverse analysis can provide useful results, Field *et al.* (1982) do point out, as does Clarke (1988a), that this type of analysis is most effective when species are strongly linked to a gradient as reflected in the station groupings. The results of the descriptive analysis clearly show this not to be the case (e.g. Table 4.8) and this conclusion is supported by the statistical results. Given that a particular taxon can appear only once in a cluster dendrogram or ordination plot, it is difficult statistically to represent the complex pattern of species distributions observed in the present study.

Results similar to those obtained at 10m in March were also obtained for the remaining inverse analyses (i.e. 30m in March and 10 and 30m in May). Given that these analyses provided little additional information to that obtained from the descriptive analyses, the results are not further reported. However, uncommon species not included in the descriptive analyses are noted, as is any species that may have value as an 'indicator'.

4.2.3.1.3 Relationship to Environmental Variables

The relationship between the environmental variables measured at 10m in March 1987 and the corresponding station ordination plot is shown in Figure 4.25. Although there was some variability, the plots for temperature (Figure 4.25a) and salinity (Figure 4.25b) showed a good visual correlation with the station clusters. Clearly, both the lowest temperatures and salinities were associated with station clusters occurring in the Firth of Clyde, with intermediate values in the North Channel and Firth of Lorn, and the highest values on the Malin Shelf. The total range in temperature and salinity was 3.42°C, and 2.98°/$_{oo}$, respectively.

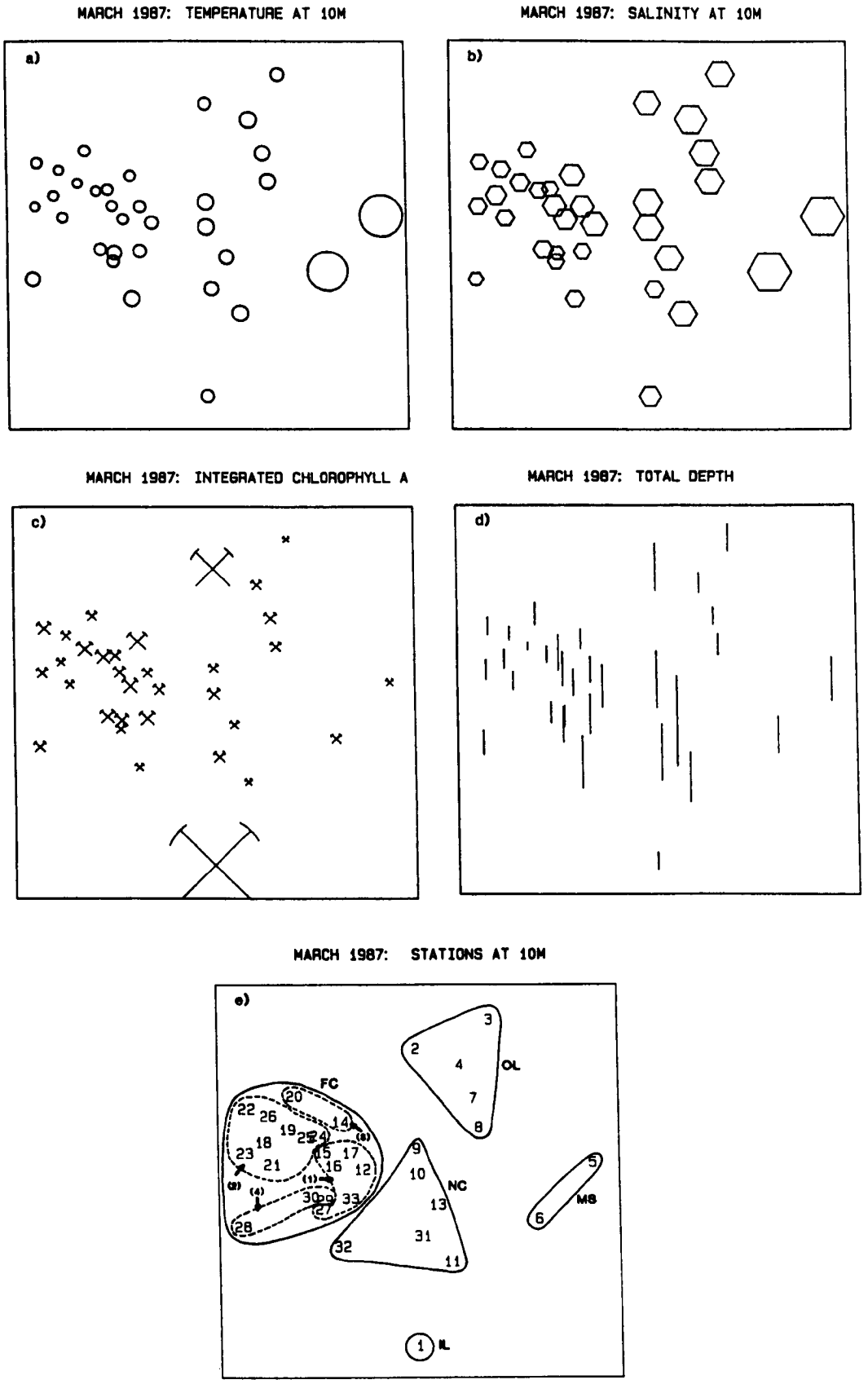


Figure 4.25 Environmental variables (a to d) measured at 10m in March 1987 and the corresponding station ordination plot (e). The symbol size shown in plots a to d reflects the variable magnitude at each station.

Phytoplankton biomass, measured as chlorophyll *a*, was generally low throughout the study area at the time of sampling (Figure 4.25c). Although values ranged from 0.09 to 1.20mg m^{-3}, the median value was 0.16mg m^{-3} and biomass exceeded 0.30mg m^{-3} at only two stations, both located in the inner Firth of Lorn: FL15 (1.29mg m^{-3}) and FL13 (0.63mg m^{-3}). In the case of station FL15 (group IL) it is difficult to comment on the importance of the high chlorophyll *a* value given that this was the only station in the IL group. Similarly, although slightly higher chlorophyll *a* levels, relative to the remaining stations, were recorded at several stations in the Firth of Clyde, no clear pattern emerged. In general, chlorophyll *a* levels throughout the study area did not appear to be of major importance in structuring the station clusters.

Although the relationship between total depth and the station clusters (Figure 4.25d) was not as clear as that for temperature and salinity, depth did appear to be correlated with certain individual groups. Stations in the North Channel group tended overall to be deeper than those in either of the four remaining station groups while those in the Firth of Clyde were all relatively shallow. The two stations occurring on the Malin Shelf were of intermediate depth. Total depth did not, however, appear to be strongly correlated with station clusters in the Firth of Lorn where a mixture of deep and shallow stations occurred together. Station depths in March 1987 ranged from 20 to 253m.

4.2.3.2 March 1987: 30m

4.2.3.2.1 Station Analysis

The results of the multivariate analyses for samples collected at 30m (Figure 4.26a and b) showed several subtle differences in station relationships compared with those observed at 10m. Stations in the Firth of Clyde and North Channel were more tightly clustered than at 10m and

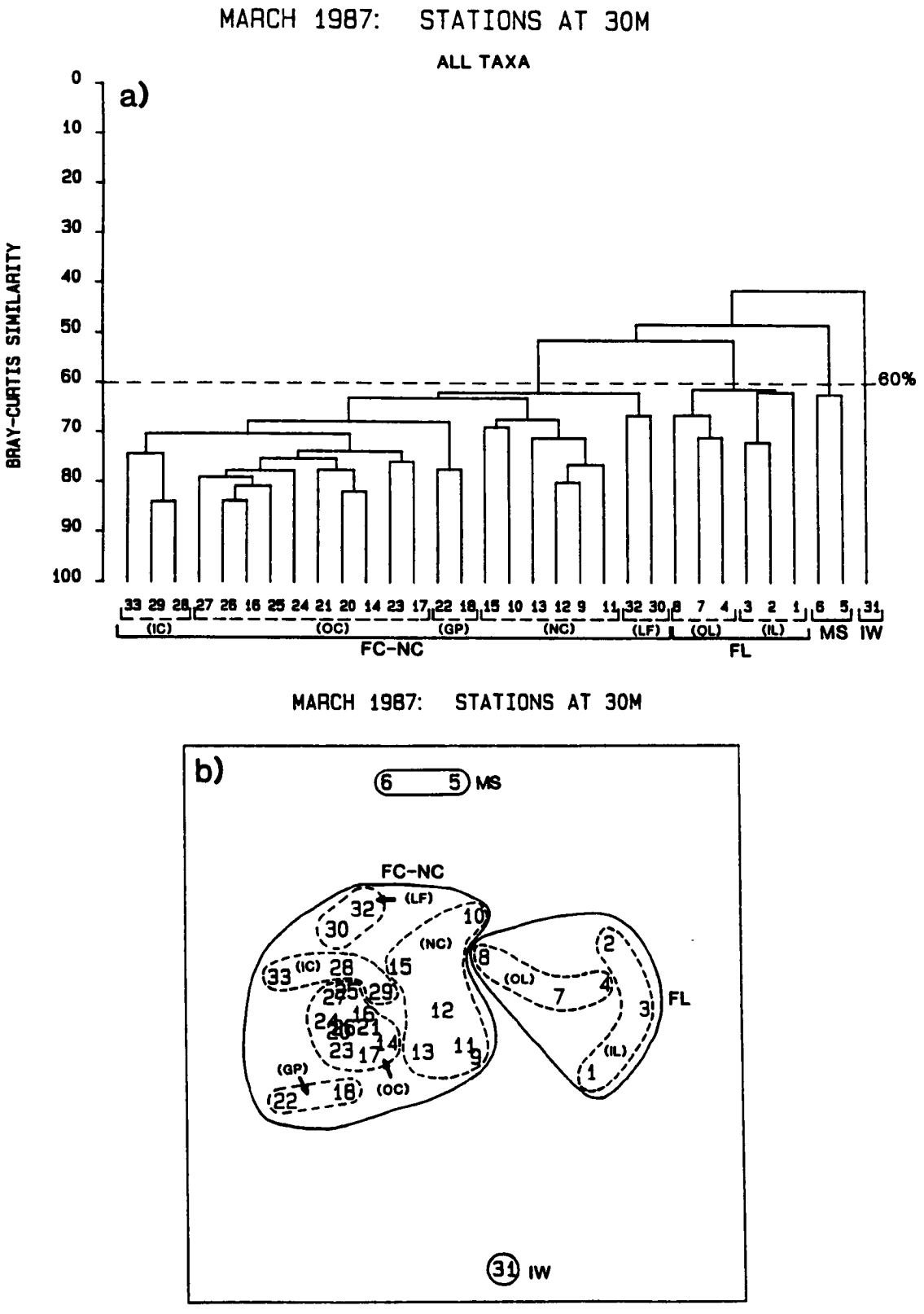


Figure 4.26 Cluster results (a) and two-dimensional MDS configuration solution (b) for analyses using all taxa collected at 10m in March 1987. IC = Inner Clyde, OC = Outer Clyde, GP = Great Plateau, NC = North Channel, LF = Loch Fyne, OL = Outer Lorn, IL = Inner Lorn, MS = Malin Shelf, IW = Inchmarnock Water, FC-NC = Firth of Clyde - North Channel, FL = Firth of Lorn.

station FL15 was now clustered with other stations in the Firth of Lorn. Four major groups could be recognized in the dendrogram plot at 60% similarity and all groups and subgroups exhibited a well-defined geographical affinity to a particular region (Figure 4.27). The first group, 'FC-NC', contained only stations in the Firth of Clyde and North Channel; the second group, 'FL', stations in the Firth of Lorn; the third group, 'MS', stations on the Malin Shelf; the fourth group, 'IW', a single station (AB38) located in Inchmarnock Water just north of Arran. These four groups could also be recognized on the ordination plot (Figure 4.26b) although the spatial separation between stations in the Firth of Lorn and the North Channel (e.g. stations D7 and C5) was much less than that at 10m. Stations in the Firth of Lorn could be further divided into an outer (OL) and an inner (IL) subgroup of stations. Within the FC-NC cluster at least five subgroups of stations could be identified and the groupings differed from those observed at 10m. Subgroups were identified for stations in the inner Clyde (IC), outer Clyde (OC), the Great Plateau (GP), the North Channel (NC) and Loch Fyne (LF). These subgroups could also be recognised on the ordination plot but tended to merge with each other. The complex nature of the inter-station relationships was reflected in the stress value of 0.17 obtained for the MDS analysis.

Cirripede nauplii were less abundant at 30m than at 10m but still comprised the most abundant taxon at 14 of 32 stations sampled, mostly located in the Firth of Lorn and North Channel. Results of the cluster and MDS ordination analyses following their removal from the data set are shown in Figures 4.28a and b. As with the pattern observed at 10m, station clusters were generally looser, particularly in the Firth of Lorn. Stations in that region were fragmented into three separate groups and station D4 previously clustered with the outer Lorn stations formed part of the North Channel group. In the Firth of Clyde, similarity between individual stations increased and stations in the North Channel,

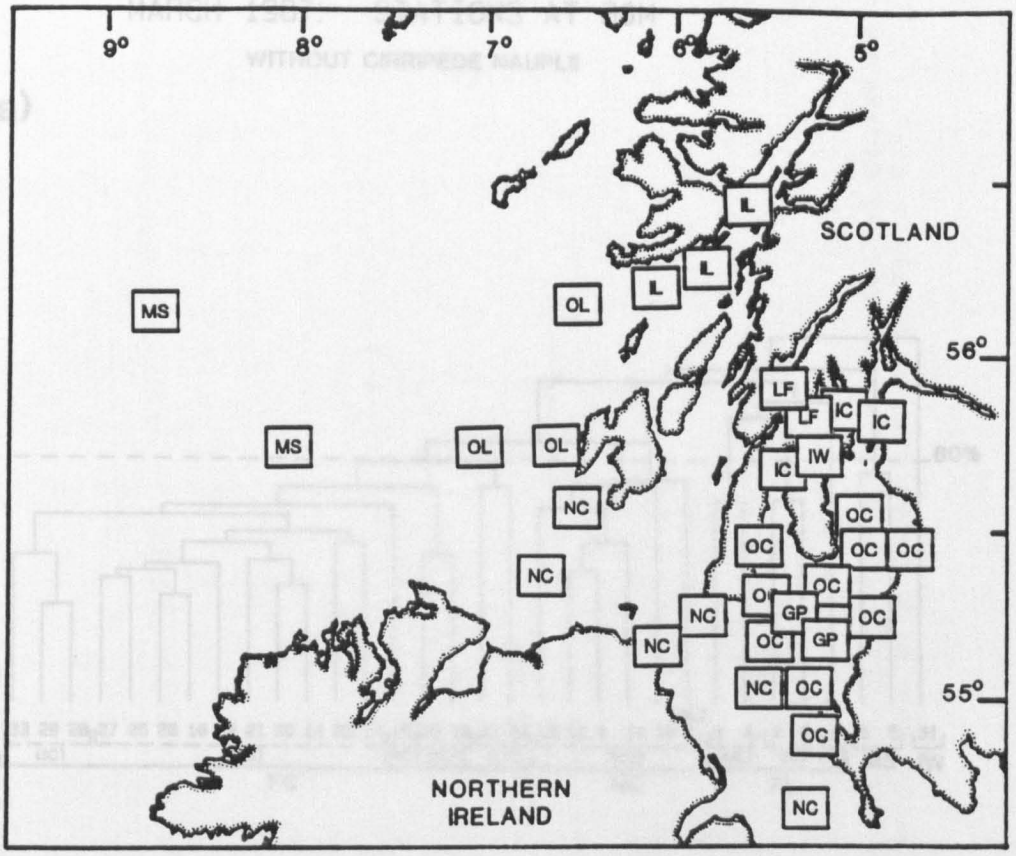


Figure 4.27 Location of station groups identified in cluster and two-dimensional MDS analyses using all taxa collected at 10m in March 1987. IC = Inner Clyde, OC = Outer Clyde, GP = Great Plateau, NC = North Channel, LF = Loch Fyne, OL = Outer Lorn, IL = Inner Lorn, MS = Malin Shelf, IW = Inchmarnock Water.

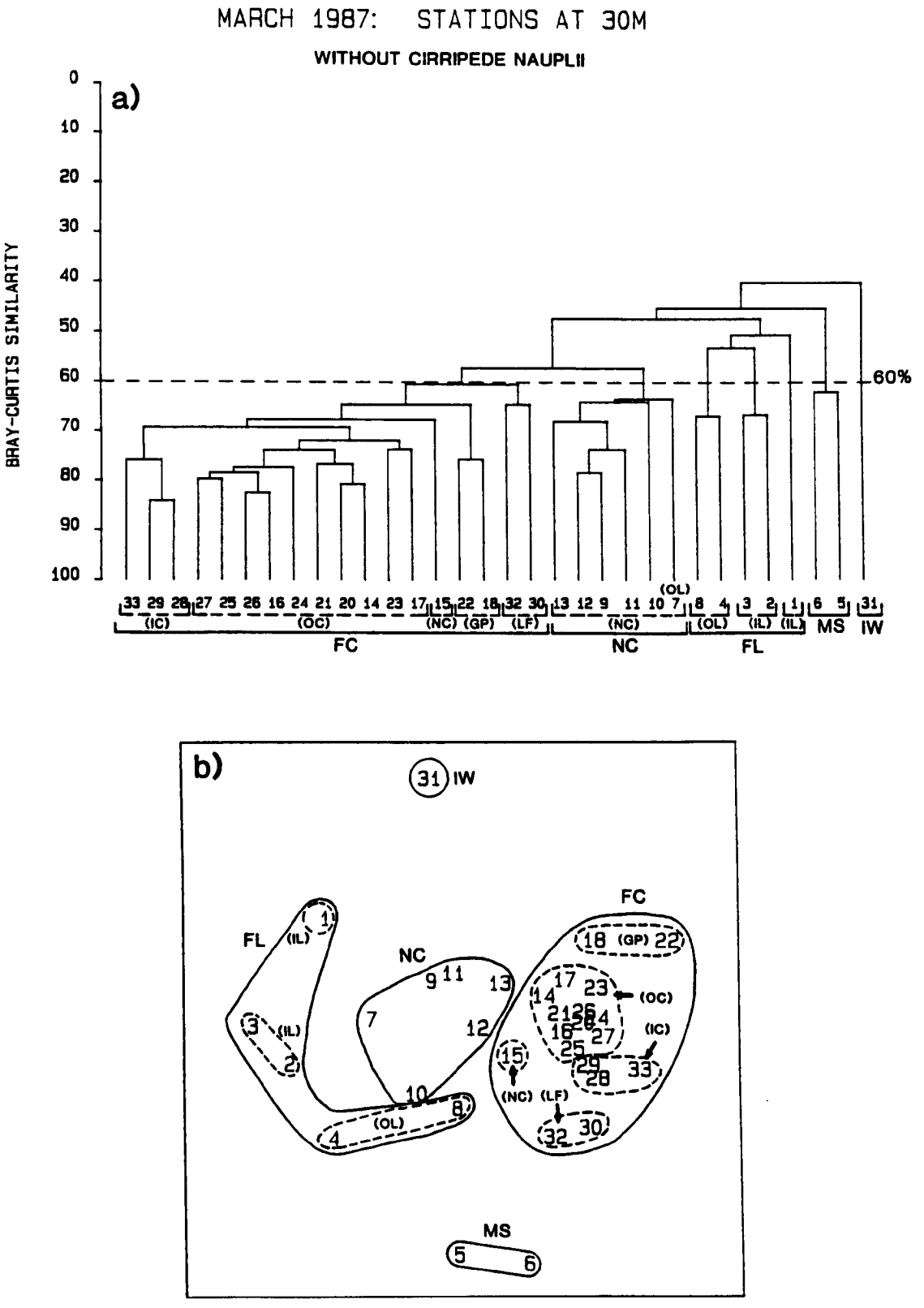


Figure 4.28 Cluster results (a) and two-dimensional MDS configuration solution (b) for analyses conducted excluding cirripede nauplii in March 1987 at 30m. Numbers enclosed in brackets (i.e. in (a)) indicate the station group in the original cluster analysis. IC = Inner Clyde, OC = Outer Clyde, GP = Great Plateau, NC = North Channel, LF = Loch Fyne, OL = Outer Lorn, IL = Inner Lorn, MS = Malin Shelf, IW = Inchmarnock Water, FC = Firth of Clyde, FL = Firth of Lorn.

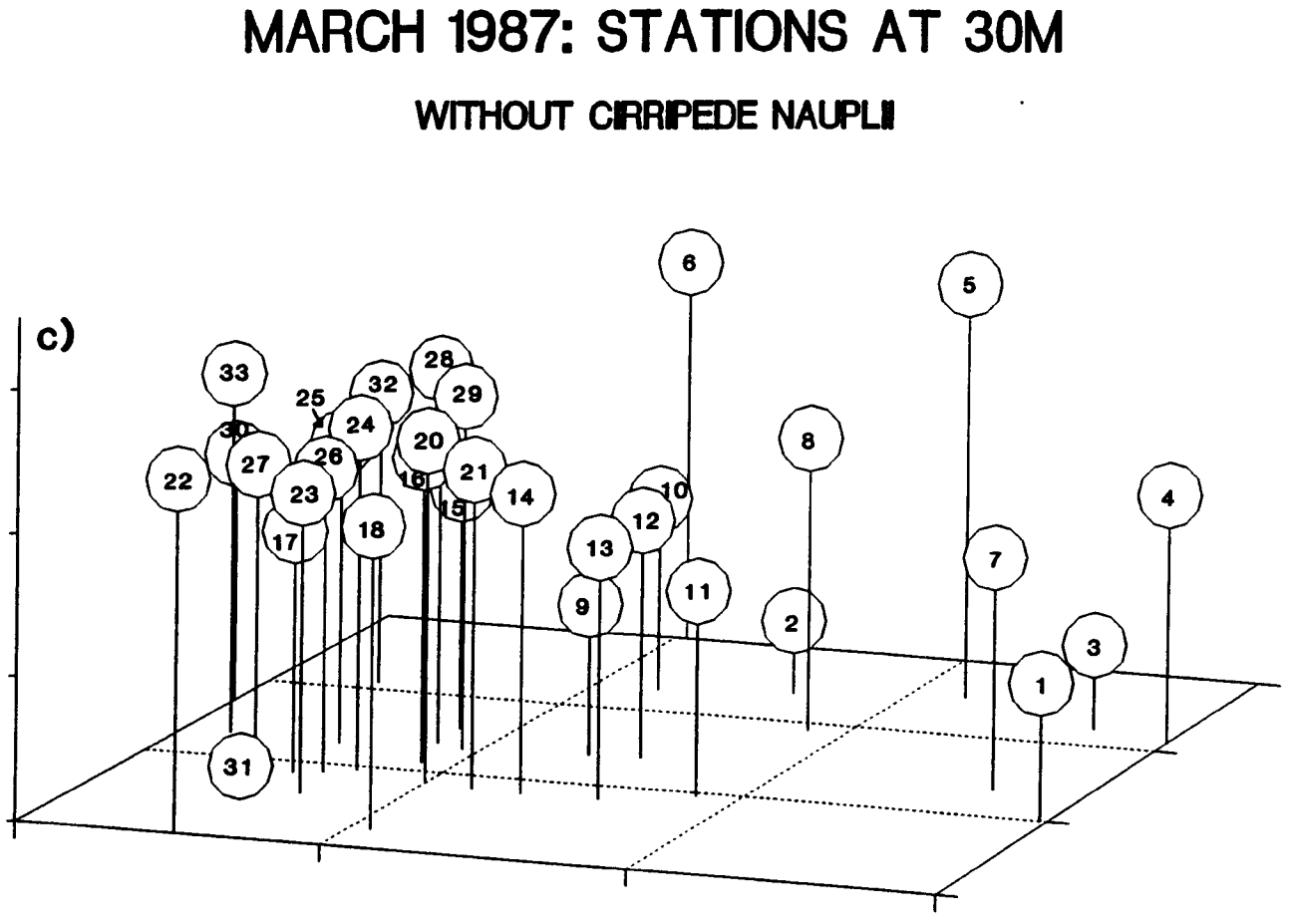


Figure 4.28 (Continued). Three-dimensional MDS configuration solution for analysis conducted excluding cirripede nauplii at 10m in March 1987. Station numbers correspond with those listed in Table 4.7.

with the exception of Y3 formed a separate cluster. Station AB38 (IW) located off the northern tip of the Island of Arran and the Malin Shelf (MS) stations remained virtually unaffected.

Separation between the station groups was poor on the corresponding MDS plot (Figure 4.28b) and this was reflected by the stress value of 0.17. The plot showed only slight spatial separation between the outer Lorn subgroup (stations D7 and FL9) and stations in the North Channel. The latter group also tended to merge with the adjacent Firth of Clyde stations. Only the Inchmarnock Water and Malin Shelf stations showed good spatial separation from the remaining groups similar to that observed in the initial analysis (Figure 4.26b).

The corresponding three-dimensional solution with a stress of 0.13 is shown in Figure 4.28c. Again, on a coarse scale the two- and three-dimensional plots show reasonable agreement. However, the plots differ in the location of station D4 which shifts from the North Channel ('NC') group in the two-dimensional ordination, to the Firth of Lorn (FL) group in the three-dimensional plot.

4.2.3.2.2 Species Analysis

Faunal assemblages for each of the nine groups or subgroups identified in the multivariate analyses are shown in Table 4.9. Once again it was subtle shifts in relative abundances, rather than changes in species composition, which seemed to be responsible for the station clusters. Most of the fauna within each group comprised only a few species and other taxa, with the overall species composition quite similar to that observed at 10m. Cirripede nauplii were still predominant throughout the entire study area, ranking first to third in overall abundance at eight of the nine station groups. In general, meroplanktonic taxa were well represented in all of the groups.

The large-scale differences in the faunal assemblages observed at

Table 4.9 Rank order abundance of species and taxa in station clusters identified using multivariate analyses, for sample at 30m in March. Only species comprising ≥ 3% of the fauna are included. Labels for station clusters correspond to those in Figure 4.26. IC = Inner Clyde; OC = Outer Clyde; GP = Great Plateau; NC = North Channel; LF = Loch Fyne; OL = Outer Lorn; IL = Inner Lorn; MS = Malin Shelf; IW = Inchmarnock Water.

IC	**OC**	**GP**	**NC**	**LF**
Cirripede nauplii	*Calanus* spp.	*Calanus* spp.	Cirripede nauplii	*Oithona* spp.
Calanus spp.	Cirripede nauplii	Cirripede nauplii	*Calanus* spp.	*Acartia clausi*
Microcalanus spp.	*Oithona* spp.	*Temora longicornis*	*Oithona* spp.	Cirripede nauplii
Temora longicornis	*Temora longicornis*		*Electra pilosa*	Polychaete larvae
Oithona spp.	*Microcalanus* spp.		*Microcalanus* spp.	*Microcalanus* spp.
Polychaete larvae	Polychaete larvae		*Temora longicornis*	*Temora longicornis*
	Acartia clausi		Polychaete larvae	*Oithona similis*
	Pseudocalanus spp.		*Acartia clausi*	*Littorina littorea*
	Electra pilosa			
OL	**IL**	**MS**	**IW**	
Cirripede nauplii	Cirripede nauplii	*Oithona* spp.	*Calanus* spp.	
Electra pilosa	*Electra pilosa*	Cirripede nauplii	*Oithona* spp.	
		Acartia clausi	*Littorina littorea*	
		Paracalanus parvus	*Calanus finmarchicus*	
		Pseudocalanus spp.	Cirripede nauplii	
		Microcalanus spp.	*Electra pilosa*	
			Opisthobranchia	

10m were generally reflected at 30m. The Firth of Clyde subgroups (IC, OC, GP, NC, IW) remained dominated by *Calanus* spp. with the exception of Loch Fyne (LF) where small copepods such as *Oithona* spp. and meroplanktonic forms predominated. It should be noted that although the Inchmarnock Water (IW) station clustered separately from the remaining Firth of Clyde stations (Figures 4.26a and b), *Calanus* spp. was still the dominant taxon. The separate clustering of this station (AB38) appears to be due to low numbers of zooplankton collected at that time relative to other stations in the Firth of Clyde (Figure 4.11a). In the Firth of Lorn (groups OL and IL) the fauna consisted almost entirely of cirripede nauplii and cyphonautes of the bryozoan, *Electra pilosa*, as was observed at 10m. *Oithona* spp. remained dominant among the small copepods common on the Malin Shelf with cirripede nauplii ranking second in overall abundance.

Eighteen species were found to characterise the fauna at 30m using inverse analysis, fifteen of which were also identified using the descriptive method. The three species omitted from Table 4.9 were *Ctenocalanus vanus* Giesbrecht, *Metridia lucens* Boeck, and *Centropages hamatus*. *C. vanus* was collected only at station D0 which formed part of the Malin Shelf group. *C. hamatus* was collected only from the North Channel group, although it is typically more widespread (see Figure 4.17j). *M. lucens* occurred in the Malin Shelf and North Channel groups.

4.2.3.2.3 Relationship to Environmental Variables

Environmental variables, superimposed onto the station ordination plot, and the original station plot, are shown in Figure 4.29 for stations sampled at 30m in March. As observed at 10m, temperature and salinity were the variables that showed the most pronounced association with the observed station clusters. Temperatures at 30m were comparable to those recorded for 10m with a maximum of 9.3°C and a minimum of

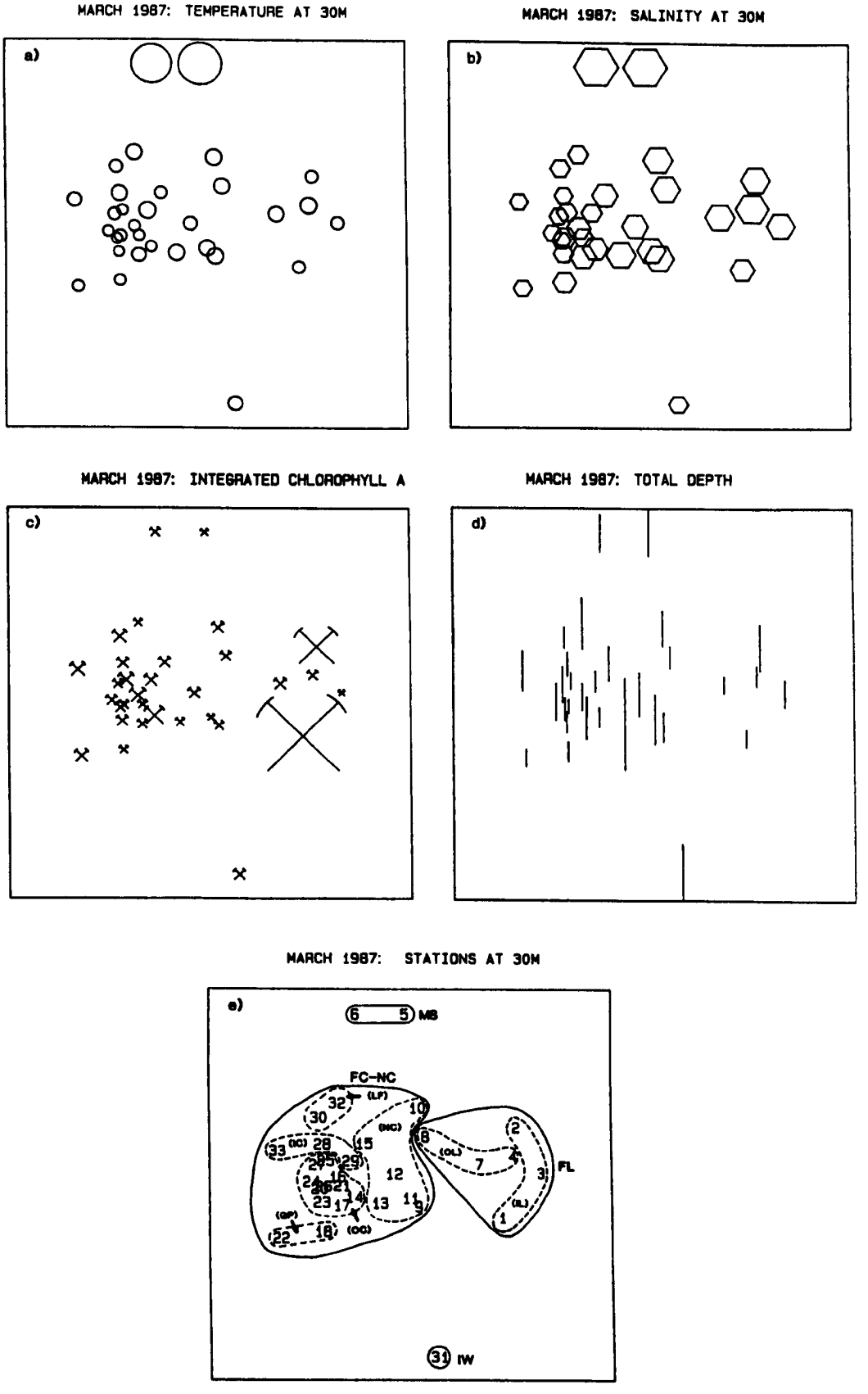


Figure 4.29 Environmental variables (a to d) measured at 30m in March 1987 and the corresponding station ordination plot (e). The symbol size shown in plots a to d reflects the variable magnitude at each station.

6.0°C. However, salinities were slightly increased at 30m occurring only between 32.8°/oo and 35.41°/oo. The total range in salinity at 30m was 2.61°/oo compared with 2.98°/oo at 10m. Although station clusters at 30m were visually correlated with changes in temperature (Figure 4.29a) the gradient at 30m was curvilinear compared with that observed at 10m (Figure 4.25a). Higher temperatures were associated with the two sub-groups located near the head of the Firth of Clyde (i.e. LF and IC) while temperatures decreased towards the mouth of the firth (i.e. groups OC and GP). Outside the Clyde, temperatures were generally higher, with maximum values occurring on the Malin Shelf. Within the Firth of Lorn, temperatures were consistently higher at the outer than the inner stations.

Changes in salinity were also visually correlated with the station clusters at 30m (Figure 4.29b) and as observed at 10m, values showed a general increase from inshore to offshore. It is interesting to note the relatively high salinities throughout the Firth of Lorn compared with stations in the Firth of Clyde. However, once again, values on the Malin shelf were markedly higher than those recorded at any of the other stations.

Neither phytoplankton biomass (Figure 4.29c) nor total depth (Figure 4.9d) appeared to have a marked effect on the station groups at this depth. Both variables were distributed throughout the station clusters in a generally random fashion. The range in values for each variable is identical to those given for 10m, with the exception that the minimum value of total depth for stations sampled at 30m was 36m.

4.2.3.3 May 1986: 10m

4.2.3.3.1 Station Analysis

Much more than in March, samples collected at 10m in May 1986

showed a high degree of spatial organisation throughout the study area. From the dendrogram plot (Figure 4.30a) five station groups could be distinguished at 60% similarity. These were designated as follows: 'LF', Loch Fyne; 'AD', Arran Deep; 'OC-NC', Outer Clyde/North Channel; 'FL', Firth of Lorn; 'MS', Malin Shelf. The stations comprising each of the groups is shown in Figure 4.31. The Loch Fyne group consisted of the one station situated in lower Loch Fyne, while the Arran Deep group contained the four stations located in the deep-water basin surrounding Arran. Although these two groups fused together at around 47% similarity they remained quite distinct from the remainder of the stations. The Outer Clyde/North Channel group contained stations located throughout the outer Firth of Clyde and the North Channel. This group could be further divided at about 65% similarity into a subgroup containing outer Firth of Clyde and North Channel stations ('MZ', Mixed Zone) north of about 55°12'N, and a smaller subgroup of stations ('NC', North Channel) situated further south in the North Channel. In general, the degree of clustering was relatively tight among the Arran Deep, Mixed Zone and North Channel stations, contrasting with more loosely clustered groups consisting of stations in the Firth of Lorn and on the Malin Shelf.

The result of the MDS ordination was in good agreement with that obtained using cluster analysis (Figure 4.30b). There was good spatial separation among the five main groups identified at 60% similarity and also the Mixed Zone - North Channel subdivision. A stress level of 0.12 was obtained for the MDS analysis indicating that the plot provides a very good representation of the inter-station relationships.

The above analyses were repeated using only the copepod fauna in an attempt to assess the degree to which their distributions and abundances reflected the overall observed patterns. (Such an analysis was unwarranted for the March cruise due to the paucity of the copepod fauna at that time.) The results of the cluster analysis (Figure 4.32a) showed a similar pattern of station groupings to those in the original

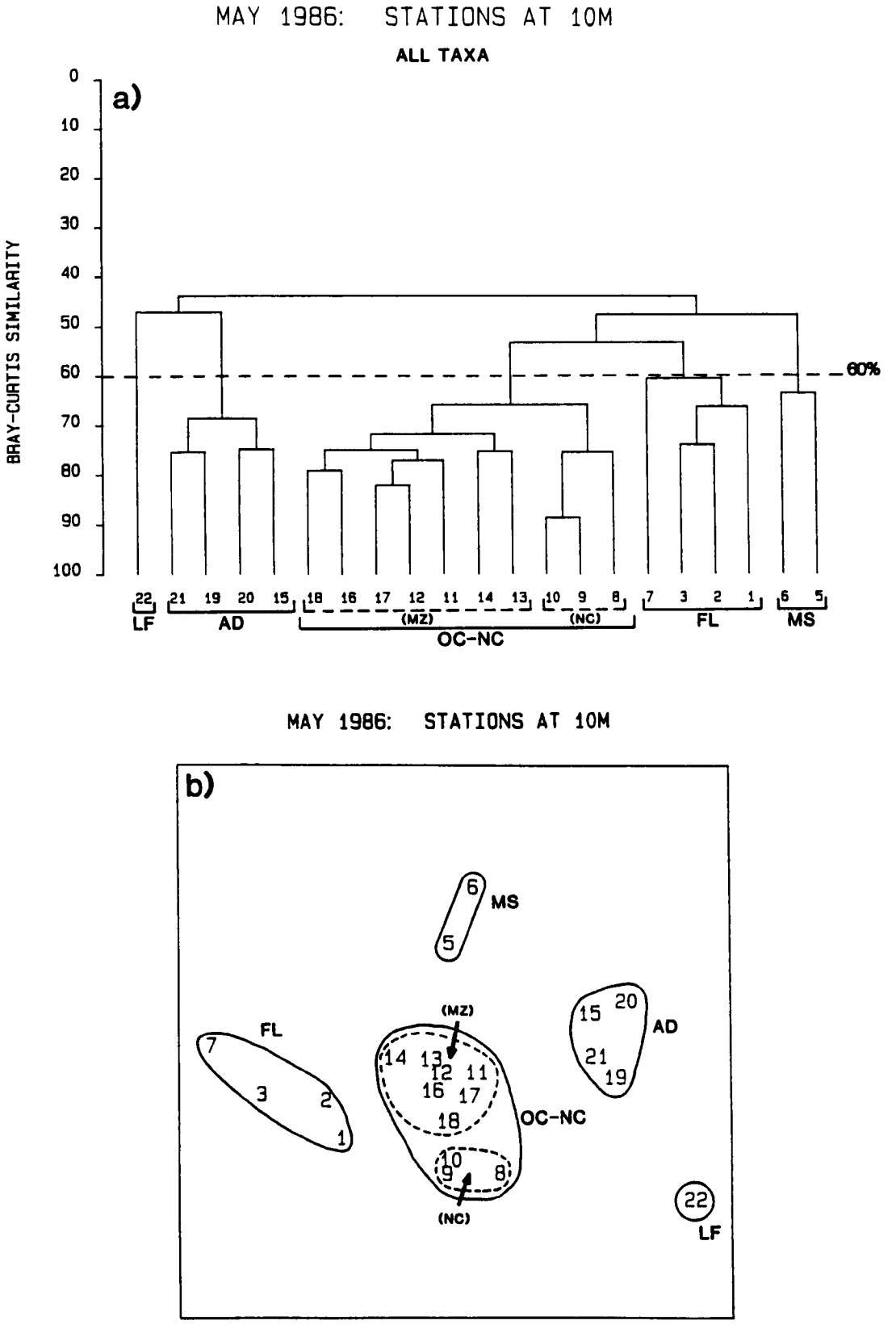


Figure 4.30 Cluster results (a) and two-dimensional MDS configuration solution (b) for analyses using all taxa collected at 10m in May 1986. LF = Loch Fyne, AD = Arran Deep, MZ = Mixed Zone, NC = North Channel, FL = Firth of Lorn, MS = Malin Shelf, OC-NC = Outer Clyde - North Channel.

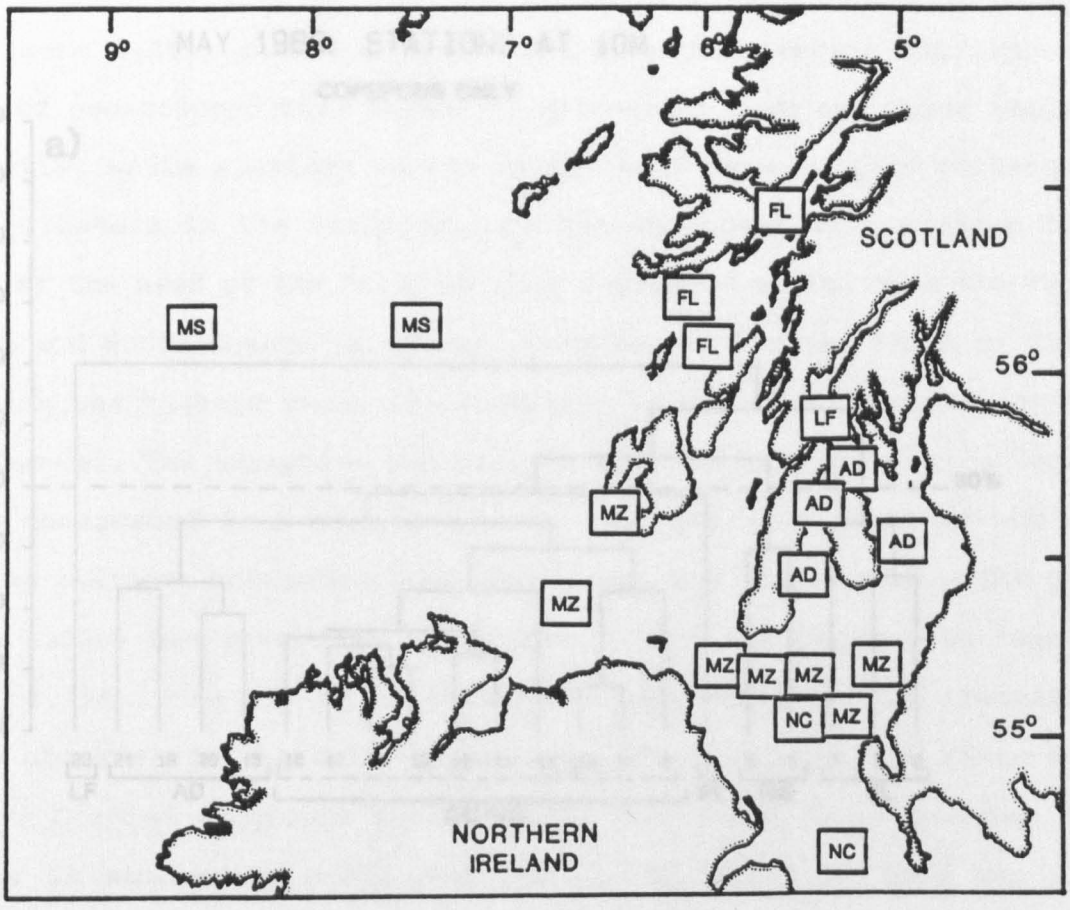


Figure 4.31 Location of station groups identified in cluster and two-dimensional MDS analyses using all taxa collected at 10m in May 1986. LF = Loch Fyne, AD = Arran Deep, MZ = Mixed Zone, NC = North Channel, FL = Firth of Lorn, MS = Malin Shelf.

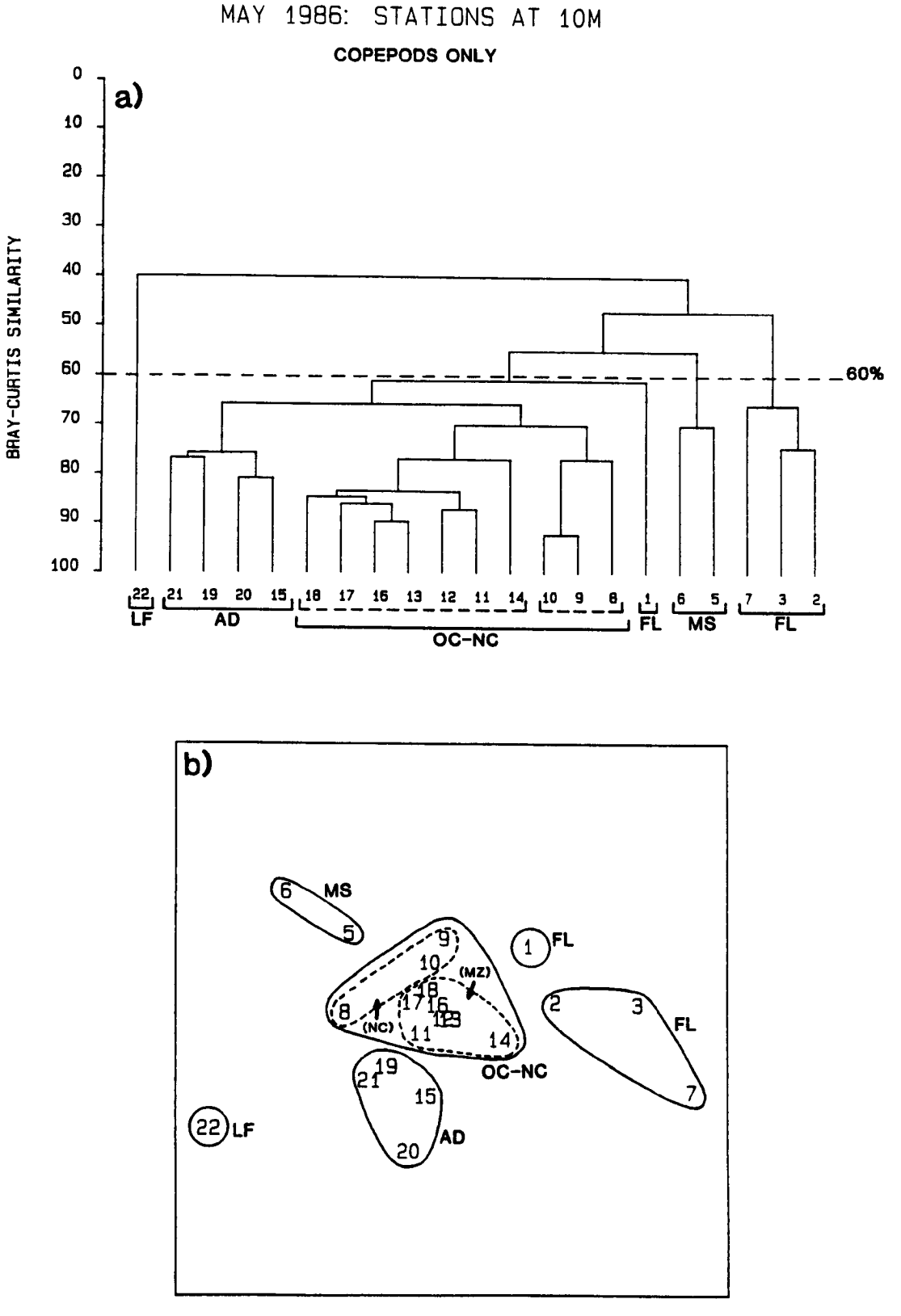


Figure 4.32 Cluster results (a) and two-dimensional MDS configuration solution (b) for analyses conducted using only copepod taxa in May 1986 at 10m. LF = Loch Fyne, AD = Arran Deep, MZ = Mixed Zone, NC = North Channel, FL = Firth of Lorn, MS = Malin Shelf, OC-NC = Outer Clyde - North Channel.

plot (Figure 4.30a) although there were some interesting differences. Removal of non-copepod taxa seemed to affect the Lorn and Clyde regions differently, while stations on the Malin Shelf were largely unchanged. Station clusters in the Firth of Lorn became looser with station FL15 located at the head of the firth showing a greater affinity to the Firth of Clyde and North Channel stations. However, within the Firth of Clyde clustering was tighter among all stations, as was also observed for the North Channel. The exception was station AB40 in Loch Fyne which became sharply demarcated from both the Arran Deep group of stations and all remaining stations throughout the study area. The corresponding MDS plot (Figure 4.32b) was generally in agreement with the dendrogram results (Figure 4.32a). The six major station groups could all be identified and, as observed in the dendrogram, similarity between the Mixed Zone and North Channel subgroups and the Arran Deep group was increased. The decrease in similarity among stations in the Firth of Lorn was also evident although the split of station FL15 from the remaining stations was not well defined. The stress value obtained for the MDS plot was 0.12 suggesting that inter-station relationships could still be well represented using only the copepod fauna.

4.2.3.3.2 Species Analysis

Species and other taxa contributing to the station clusters in May at 10m (Table 4.10) were both similar and different to those observed at 10m in March (Table 4.8). In the inner Firth of Clyde (i.e. groups LF and AD), the fauna was largely dominated by *Calanus* with high numbers of *Pseudocalanus* spp. in both groups. In the Arran Deep, *Calanus finmarchicus* ranked third in overall abundance. *Calanus* spp. was also dominant in the Mixed Zone region although copepods such as *Oithona* spp. and *Acartia clausi*, not common in the inner Firth of Clyde, were also abundant. Species composition in the Mixed Zone and North Channel groups

Table 4.10 Rank order abundance of species and taxa in station clusters identified using multivariate analyses, for samples at 10m in May. Only species comprising ≥ 3% of the fauna are included. Labels for station clusters correspond to those in Figure 4.30. LF = Loch Fyne; AD = Arran Deep; MZ = Mixed Zone; NC = North Channel; FL = Firth of Lorn; MS = Malin Shelf.

LF	**AD**	**MZ**
Calanus spp.	*Calanus* spp.	*Calanus* spp.
Pseudocalanus spp.	*Pseudocalanus* spp.	*Temora longicornis*
Temora longicornis	*Calanus finmarchicus*	*Pseudocalanus* spp.
		Oithona spp.
		Acartia clausi
		Evadne nordmanni
NC	**FL**	**MS**
Temora longicornis	*Podon leuckartii*	*Oithona* spp.
Pseudocalanus spp.	*Acartia clausi*	*Pseudocalanus* spp.
Acartia clausi	Cyprids	*Calanus* spp.
Calanus spp.	*Evadne nordmanni*	*Acartia clausi*
Evadne nordmanni	*Calanus* spp.	*Calanus finmarchicus*
Centropages hamatus	Cirripede nauplii	*Paracalanus parvus*
	Centropages hamatus	*Oithona similis*
	Pseudocalanus spp.	
	Temora longicornis	

was quite similar, but with subtle shifts in relative abundances of species. On the Malin Shelf, *Oithona* spp. was still the most abundant species with the remainder of the fauna composed of six copepod species, including *Calanus finmarchicus*. Cirripede nauplii were no longer common members of the shelf fauna.

The main difference in the faunal composition between the March and May cruises was that almost all of the species common in May were holoplanktonic. Only in the Firth of Lorn were meroplanktonic taxa, i.e. cirripede nauplii and cyprids, still common in the fauna. Two cladocerans, *Podon leuckartii* and *Evadne nordmanni*, not collected in March, were also common members of the fauna with the former replacing cirripede nauplii as the most abundant species. Of most interest,

however, was the fact that the copepod, *Acartia clausi*, was ranked second in overall abundance and four other species, *Calanus* spp., *Centropages hamatus*, *Pseudocalanus* spp., and *Temora longicornis*, none of which was common in March, were common members of the fauna in May.

Three taxa, in addition to the 13 shown in Table 4.10, were identified by the inverse analysis as being characteristic of the fauna at 10m in May. These were *Electra pilosa* cyphonautes, *Microcalanus* spp. and brachyuran zoeae. *Microcalanus* spp. occurred in both the Arran Deep and Mixed Zone groups while brachyuran zoeae were found in both the North Channel and Firth of Lorn groups. Only *E. pilosa* was restricted to a single station group, namely the Mixed Zone, but given what is likely to be a highly variable and seasonally dependent distribution pattern, this species should not be regarded as exclusive to this area.

4.2.3.3.3 Relationship to Environmental Variables

Environmental variables measured in May at 10m are superimposed onto the station ordination plot in Figure 4.33. Salinity was most closely correlated visually with the observed clustering of stations (Figure 4.33b). Temperature appeared to be important only in separating the Malin Shelf station group (Figure 4.33a), while neither values of chlorophyll *a* (Figure 4.33c) nor of total depth (Figure 4.33d) showed strong coherence with any of the station clusters (Figure 4.33e).

Salinities overall were slightly lower (31.91°/∞ to 35.29°/∞) than in March. Reduced salinities were clearly associated with stations in the inner Firth of Clyde (i.e. groups AD and LF) while high salinities were characteristic of the Malin Shelf. Salinity did not appear to be an important factor in distinguishing between stations in the outer Firth of Clyde and North Channel nor in the Firth of Lorn.

Temperatures in May at 10m were slightly warmer than those recorded at the same depth in March and the total range was only 2.55

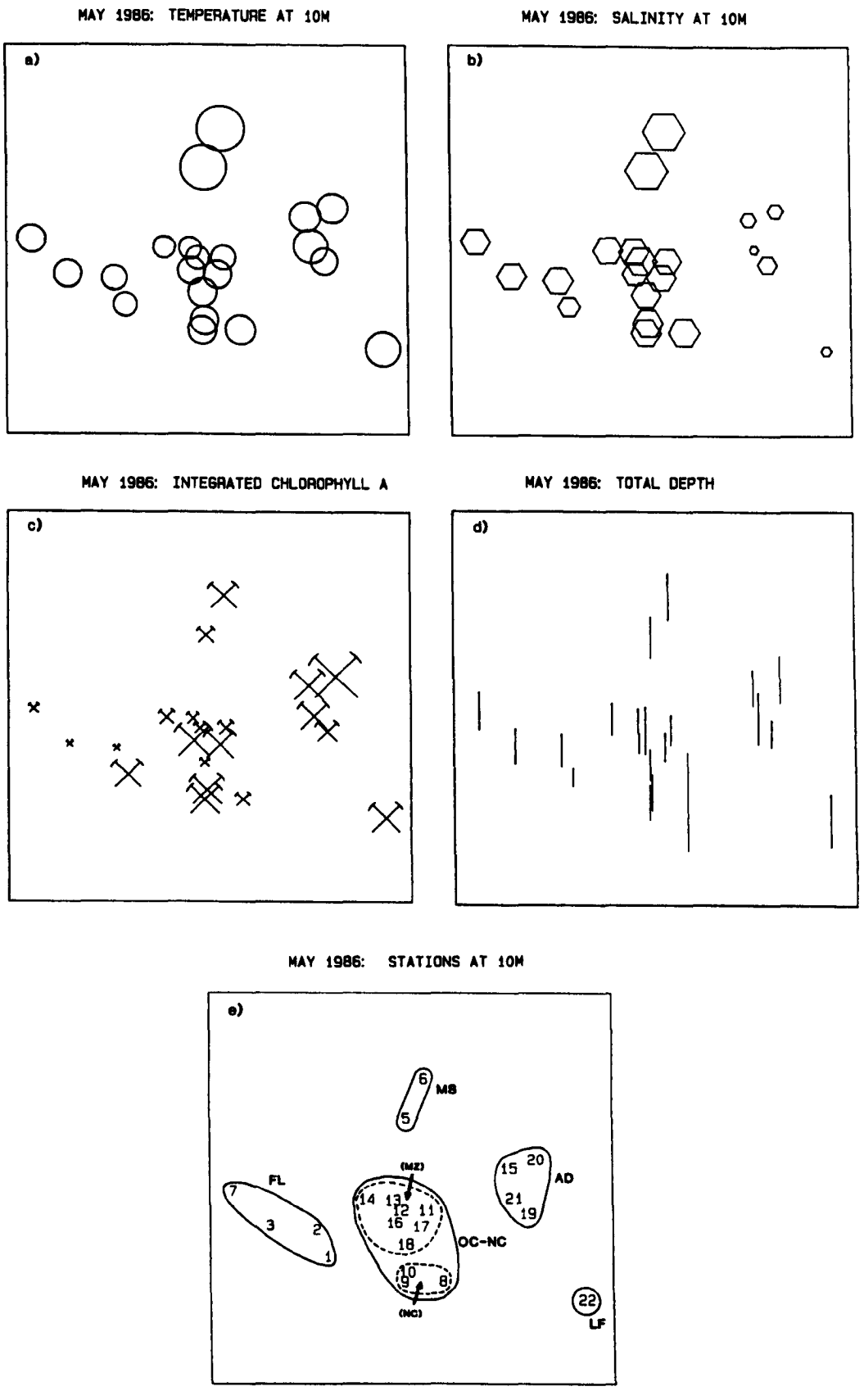


Figure 4.33 Environmental variables (a to d) measured at 10m in May 1986 and the corresponding station ordination plot (e). The symbol size shown in plots a to d reflects the variable magnitude at each station.

C°; i.e. from 7.18°C to 9.73°C. The small range in temperatures was reflected by a weaker gradient in the temperature plot (Figure 4.33a) compared with that observed at the same depth in March (Figure 4.25a). Only the Malin Shelf stations were clearly separate from all others on both occasions.

Measurements of integrated chlorophyll *a* were higher overall in May (median = 0.30) than in March (median = 0.16), although the maximum level attained was considerably lower (cf. Figures 4.25c and 4.33c). It is, however, interesting to note that, whereas the highest levels of chlorophyll *a* were recorded in the Firth of Lorn in March, the reverse occurred in May. In May, the highest level of integrated chlorophyll *a*, 0.76mg m^{-3}, occurred at station AB44 in Kilbrannan Sound while the minimum value, 0.09mg m^{-3}, occurred at station FL12 in the Firth of Lorn. In general, most station clusters contained a wide range of values, although at stations in the Firth of Lorn, except FL15, these were relatively low.

No clear relationship emerged between total depth and station clusters at 10m. Station depths in May ranged from 48 to 274m, and most clusters contained stations of various depths (Figure 4.33d).

4.2.3.4 May 1986: 30m

4.2.3.4.1 Station Analysis

Samples collected at 30m (Figure 4.34a) clustered into fewer groups than at 10m (Figure 4.30a). Only four groups were discernible at the 60% similarity level namely: 'AD', Arran Deep; 'MZ', Mixed Zone; 'OL', Outer Lorn; 'MS', Malin Shelf. There were two main differences in the dendrogram structure at 30m compared to 10m. These were that 1) the station in Loch Fyne clustered tightly with the Arran Deep stations, and 2) stations in the outer Firth of Clyde and North Channel were not

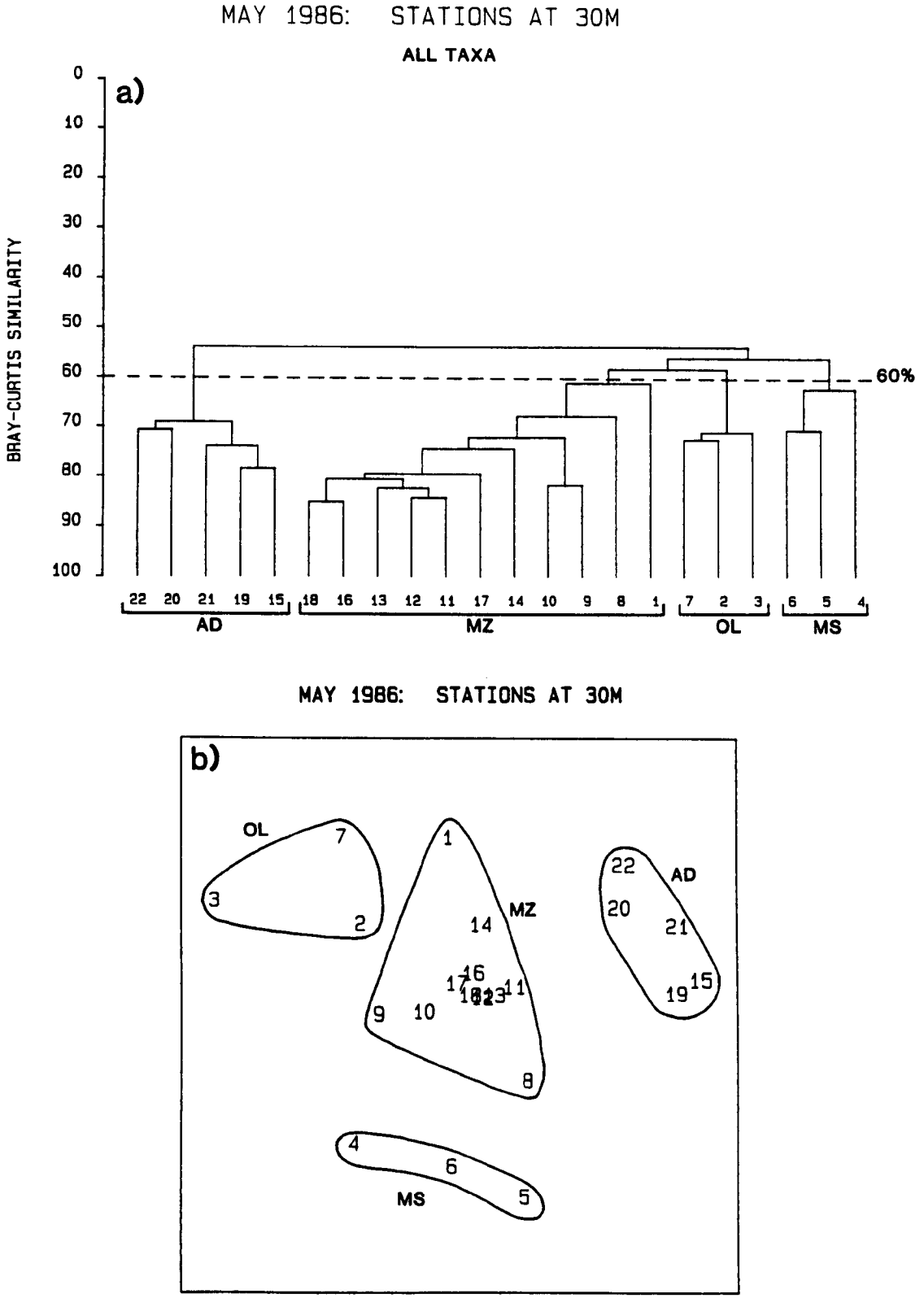


Figure 4.34 Cluster results (a) and two-dimensional MDS configuration solution (b) for analyses using all taxa collected at 30m in May 1986. AD = Arran Deep, MZ = Mixed Zone, OL = Outer Lorn, MS = Malin Shelf.

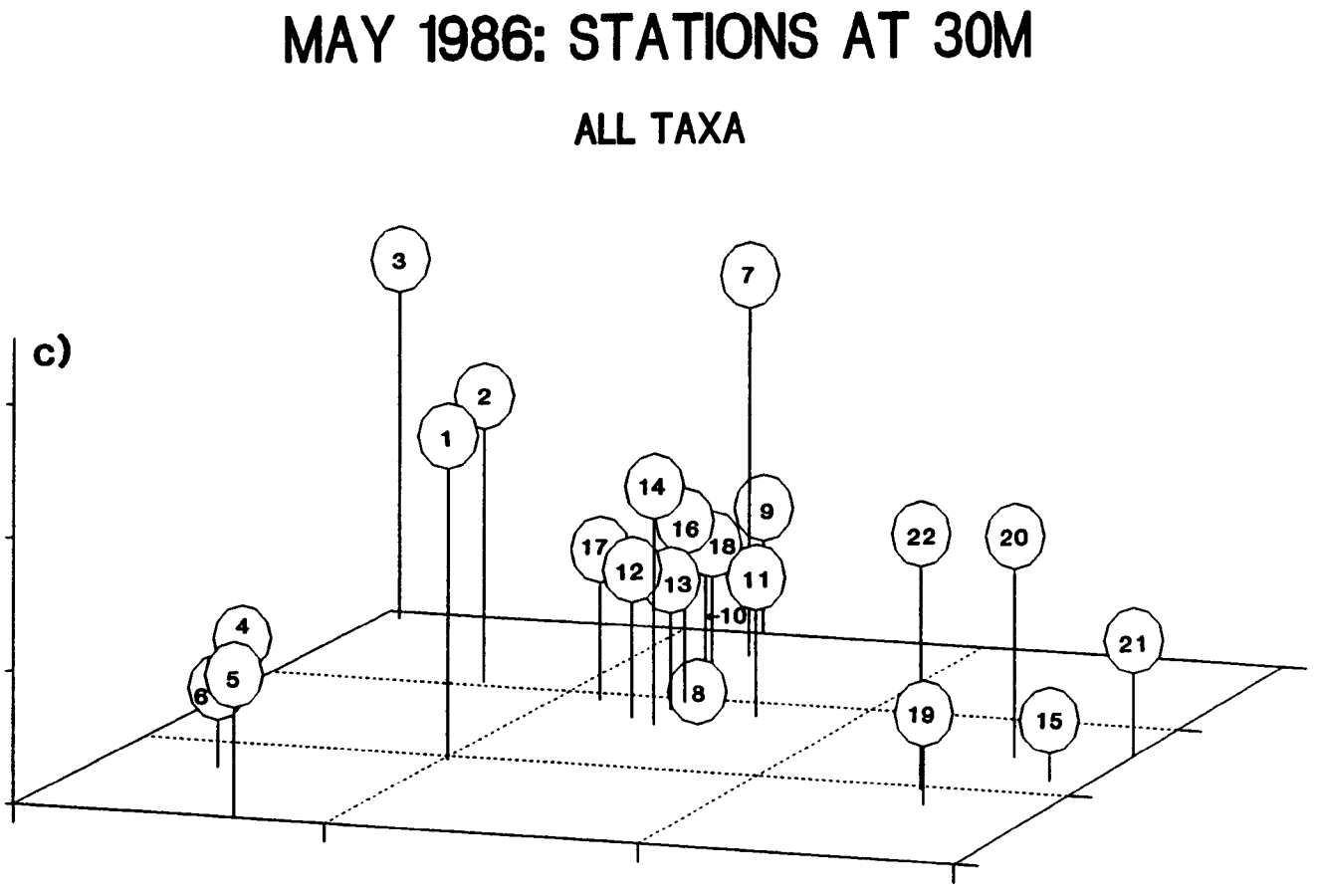


Figure 4.34 (Continued). Three-dimensional MDS configuration solution for analysis conducted using all taxa at 30m in May 1986. Station numbers correspond with those listed in Table 4.7.

readily distinguishable into two groups. The Arran Deep, Outer Lorn and Malin Shelf groups were similar to those observed at 10m, although station FL15 located in the inner Firth of Lorn was weakly linked with stations in the Mixed Zone group. A map of the study area showing stations within each of the clusters is given in Figure 4.35.

Stations throughout the outer Firth of Clyde and North Channel were intermingled in the MDS ordination plot (Figure 4.34b) and this may have contributed to the higher stress level of 0.15. Superimposing station clusters at the 60% similarity level onto the ordination plot clearly demarcated the Arran Deep, Outer Lorn and Malin Shelf groups from the rather nebulous Mixed Zone cluster. Stations Z4 and FL15 which were last to fuse with the cluster (Figure 4.34a) appeared on the MDS plot to be less similar to the remaining stations in that group.

The corresponding three-dimensional solution is shown for comparison in Figure 4.34c. Despite the much lower stress value of 0.08, the three-dimensional plot showed a similar arrangement of stations to that in the two-dimensional plot. In general, this was true for all three-dimensional solutions examined.

The above analyses were repeated using only the copepod fauna (Figures 4.36a and b). As observed at 10m, the overall degree of clustering among stations in the Firth of Clyde and North Channel was tighter. Only two groups could be distinguished at 60% similarity; interestingly, the split was between the Outer Lorn group and all remaining stations. The four groups (AD, MZ, MS and OL) identified in the initial analyses (Figures 4.34a and b) still occurred at about 65% similarity although station relationships within the groups was altered in some cases. Overall, stations within the Outer Lorn and Malin Shelf groups remained unchanged although, as previously noted, the Malin Shelf stations were more similar to those in the Mixed Zone group than were those in the Outer Lorn.

In the dendrogram produced using only the copepod fauna (Figure

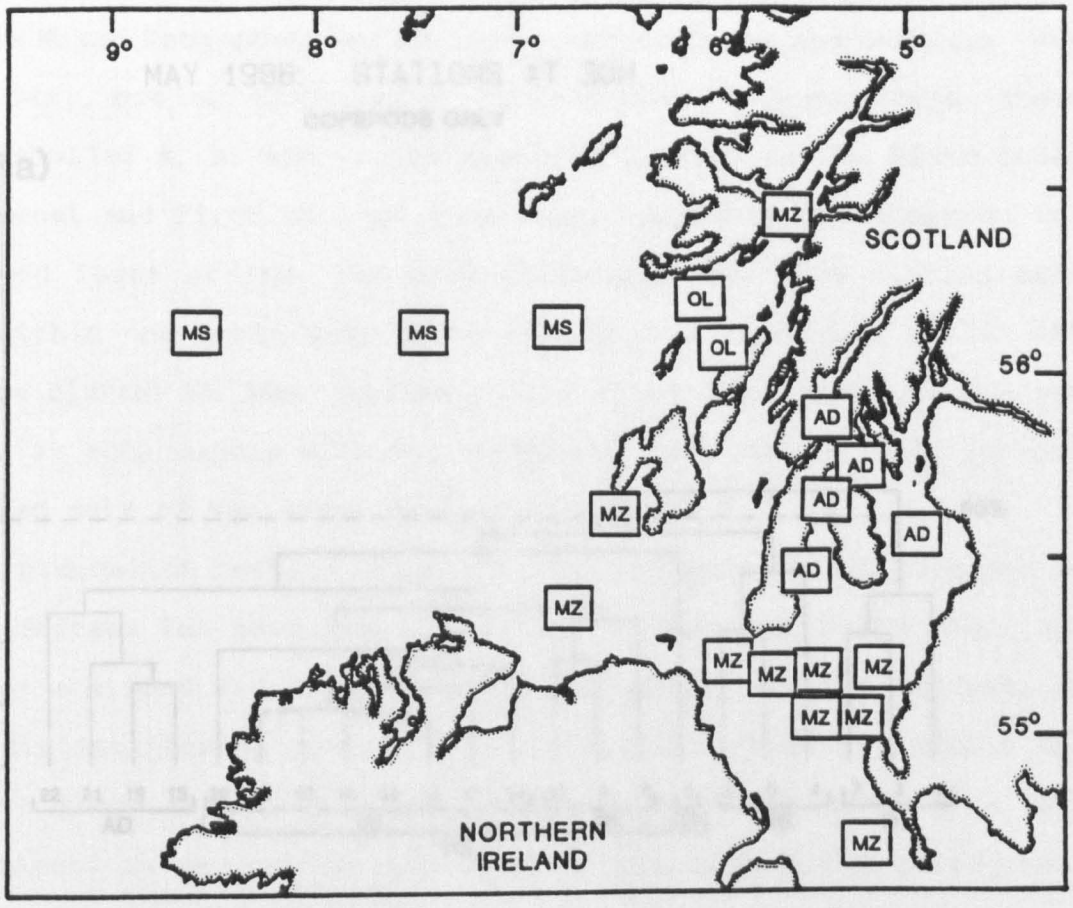


Figure 4.35 Location of station groups identified in cluster and two-dimensional MDS analyses using all taxa collected at 30m in May 1986. AD = Arran Deep, MZ = Mixed Zone, OL = Outer Lorn, MS = Malin Shelf.

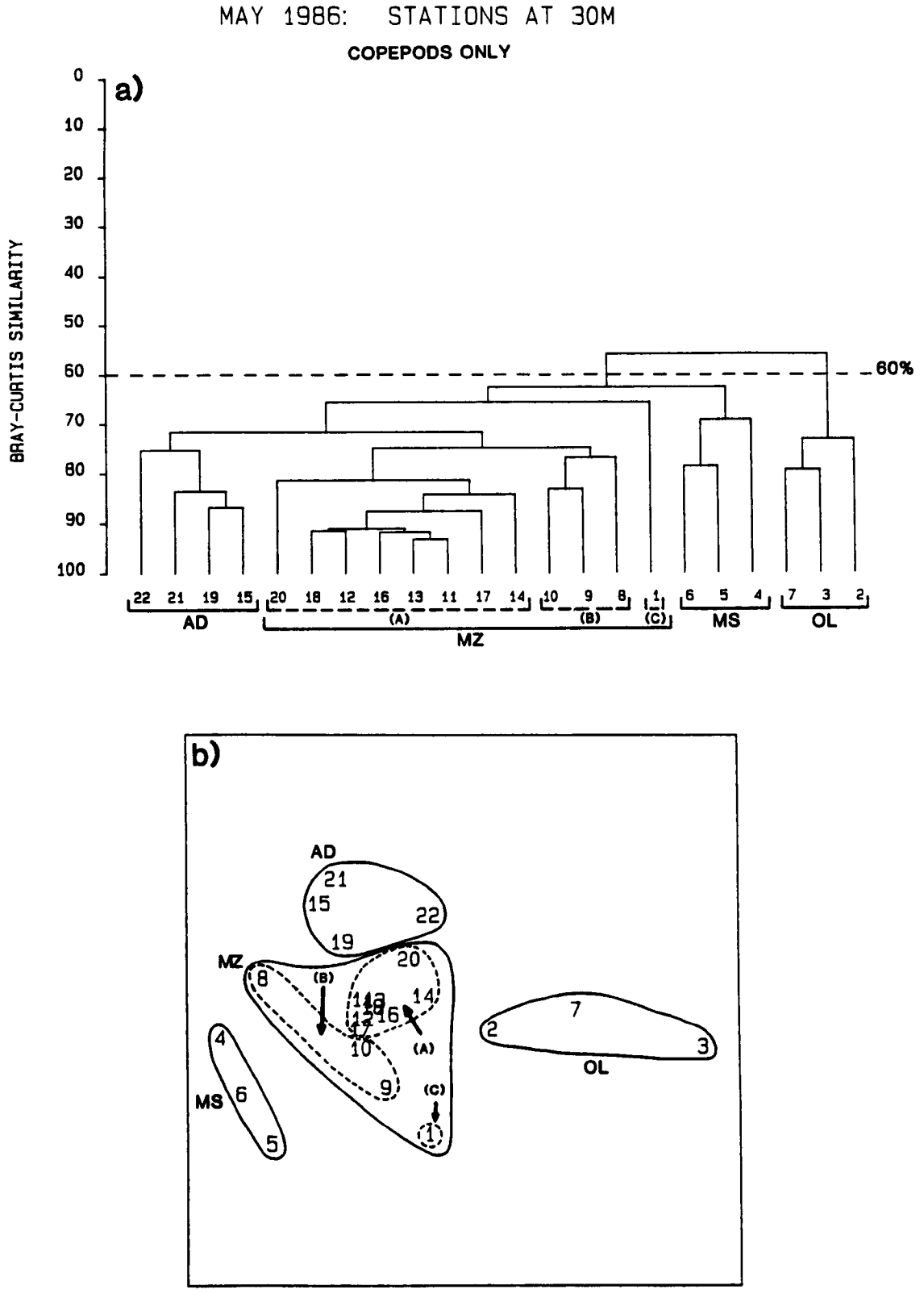


Figure 4.36 Cluster results (a) and two-dimensional MDS configuration solution (b) for analyses conducted using only copepod taxa in May 1986 at 30m. AD = Arran Deep, MZ = Mixed Zone, OL = Outer Lorn, MS = Malin Shelf. A,B, and C designate subgroups within the Mixed Zone group.

4.36a) the Mixed Zone group was no longer rather large and nebulous (see Figure 4.34a), but was comprised of three well-defined subgroups. These groups, labelled A, B, and C, corresponded closely to the Mixed Zone, North Channel and Firth of Lorn subgroups, respectively, observed for the copepod fauna at 10m. The only difference was that station AB44 located within the Arran Deep group at 10m, was contained within the Mixed Zone cluster at 30m. Similarly, the Arran Deep station group was identical at both depths with the exception that station AB40 in Loch Fyne formed part of the Arran Deep group at 30m.

The ordination results (Figure 4.36b) reflected these clusters to a lesser degree. The increased similarity between the Malin Shelf and Arran Deep stations and those in the Mixed Zone group was evident, as was the distinctiveness of the Outer Lorn group. However, within the Mixed Zone group the three subgroups apparent in the dendrogram were less distinct. In fact, there was little difference in the arrangement of stations which comprised subgroup 'B' in Figure 4.36a, between the two ordination plots (Figures 4.34b and 4.36b). A stress value of 0.13 was recorded for the analysis.

4.2.3.4.2 Species Analysis

Faunal assemblages for station clusters in May at 30m are shown in Table 4.11. As at 10m, all of the species common at 30m were holoplanktonic with the exception of cirripede nauplii and cyprids. In the inner Firth of Clyde (group AD), the fauna remained dominated by *Calanus*, including large numbers of C5's and adults (i.e. *C. finmarchicus*). In comparison, smaller copepods such as *Temora longicornis*, and *Pseudocalanus* spp. predominated in the Mixed Zone although *Calanus* spp. ranked third in overall abundance. In the outer Firth of Lorn, meroplankton in the form of cirripede nauplii and cyprids were still present as common representatives in the fauna, cyprids

Table 4.11 Rank order abundance of species and taxa in station clusters identified using multivariate analyses, for samples collected at 30m in May. Only species comprising ≥ 3% of the fauna are included. Labels for station clusters correspond to those in Figure 4.34. AD = Arran Deep; MZ = Mixed Zone; OL = Outer Lorn; MS = Malin Shelf.

AD	**MZ**	**OL**
Calanus spp.	*Temora longicornis*	Cyprids
Calanus finmarchicus	*Pseudocalanus* spp.	*Acartia clausi*
Acartia clausi	*Calanus* spp.	*Pseudocalanus* spp.
Centropages hamatus	*Acartia clausi*	*Temora longicornis*
Pseudocalanus spp.	*Oithona* spp.	Cirripede nauplii
	Evadne nordmanni	*Podon leuckartii*
		Calanus spp.
		Centropages hamatus

MS
Calanus spp.
Oithona spp.
Pseudocalanus spp.
Acartia clausi
Paracalanus parvus

ranking first in overall abundance. However, *Acartia clausi* remained the second most abundant species, and four other copepod species were also common in the fauna. On the Malin Shelf, Calanus spp. replaced *Oithona* spp. as the most abundant species, although small copepods were prominent. Meroplanktonic species were not common on the shelf, as was observed at 10m.

Three species and one taxon identified using inverse analysis were not represented in the descriptive results. These were *Oithona similis*, *Microcalanus* spp., *Electra pilosa*, and brachyuran zoeae. *E. pilosa* was largely restricted to the Mixed Zone and brachyuran zoeae to the Outer Lorn, though they did occur elsewhere at abundances below the 3% cut-off limit. *O. similis* and *Microcalanus* spp. each occurred in two areas. All four taxa occurred in relatively low numbers.

4.2.3.4.3 Relationship to Environmental Variables

At 30m in May, the strongest visual correlation between an environmental variable and the clustering of stations was again observed for salinity (Figure 4.37b). However, both temperature and chlorophyll also appeared to be visually correlated with at least one or more of the station groups (Figures 4.37a and c).

The salinity pattern at 30m was similar to that at 10m. Stations in the inner Firth of Clyde had relatively low salinities while the highest salinities were found at stations on the Malin Shelf (Figure 4.37b). However, in the Mixed Zone and the Firth of Lorn, stations could not be distinguished on the basis of salinity alone. Overall values in the study area range from 32.58°/$_{oo}$ to 35.26°/$_{oo}$.

Temperature was also similar to that observed at 10m. Once again the highest temperatures occurred on the Malin Shelf (Figure 4.37a) while elsewhere temperatures showed little difference. Temperatures at 30m in May ranged from 7.07°C to 9.61°C. These values were virtually identical to those measured at 10m.

Phytoplankton biomass also appeared to show a relationship to the clustering of stations. At 30m in May, stations in the outer Firth of Lorn all showed low levels of chlorophyll *a*, relative to those measured elsewhere throughout the study area (Figure 4.37c). One exception was at station FL8, which formed part of the Malin Shelf cluster, where a low chlorophyll *a* value was also recorded. Total depth did not bear a strong relationship with any of the station clusters observed at 30m (Figure 4.37d).

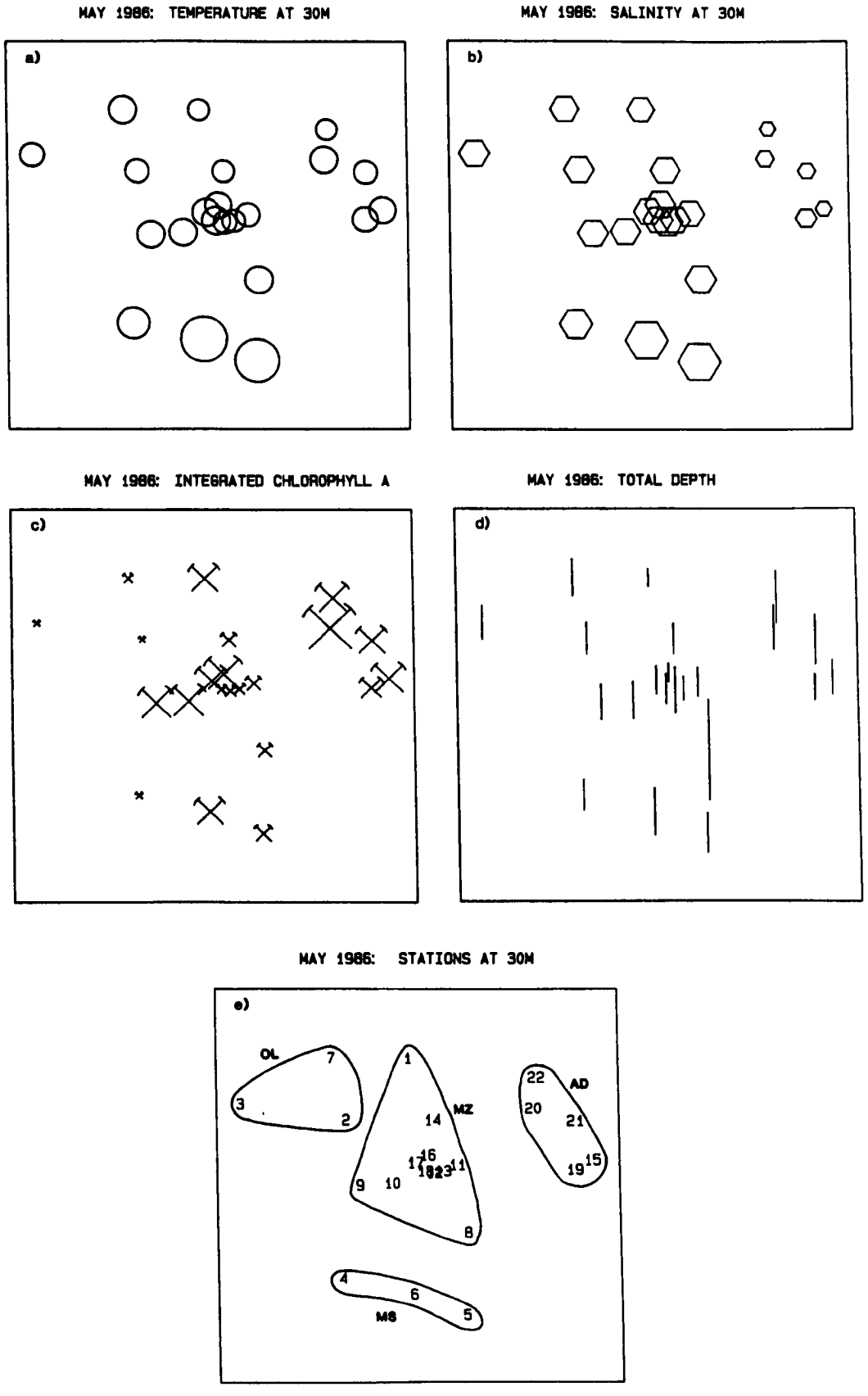


Figure 4.37 Environmental variables (a to d) measured at 30m in May 1986 and the corresponding station ordination plot (e). The symbol size shown in plots a to d reflects the variable magnitude at each station.

4.2.4 Biomass and Size Analyses

4.2.4.1 Biomass Partitioning Between Cruises

Biomass partitioning among taxa was examined between cruises using the image analysis data collected for samples at 10 and 30m during the March and May cruises (Figures 4.38 and 4.39). All biomass is expressed as volume l^{-1}, although an approximate conversion to dry weight or carbon can be made using the conversion ratios given in section 3.2.1.

In March, both the abundance and biomass of plankton were low (Figure 4.38). At 10m, total biomass was estimated at 2.73mm^3 l^{-1} with a corresponding abundance of 49 animals l^{-1}. Although 13 taxa together comprised 95% of the biomass, 76% was contributed by only three: cirripede nauplii, *Calanus* spp. and copepod nauplii; these were also the most abundant taxa collected. The remaining taxa consisted of a mixture of copepods, eggs and nauplii, and larger animals such as *Sagitta elegans* Verrill and *Parathemisto gracilipes* (Norman). Each species or other taxon contributed only a small portion (< 3% or 0.10mm^3 l^{-1}) to the total biomass.

At 30m, a similar picture was observed. Total biomass was low, estimated at 2.13mm^3 l^{-1} with a total number of 39 animals l^{-1}. Although 95% of the total biomass consisted of 15 different taxa, 77% was contributed by *Calanus* spp., cirripede and copepod nauplii. Cirripede nauplii remained the most abundant group collected, but ranked second in overall biomass to *Calanus* spp. at the 30m stations. As observed at 10m, the remaining taxa were composed of a mixture of copepods, nauplii and eggs, and larger, less abundant species such as *Sagitta elegans* and *Parathemisto abyssorum* Boeck.

In May, biomass was high and only a few taxa contributed to 99% of the estimated total at both 10m and 30m (Figure 4.39). At 10m, total biomass was estimated at 306mm^3 l^{-1} and the total number of animals

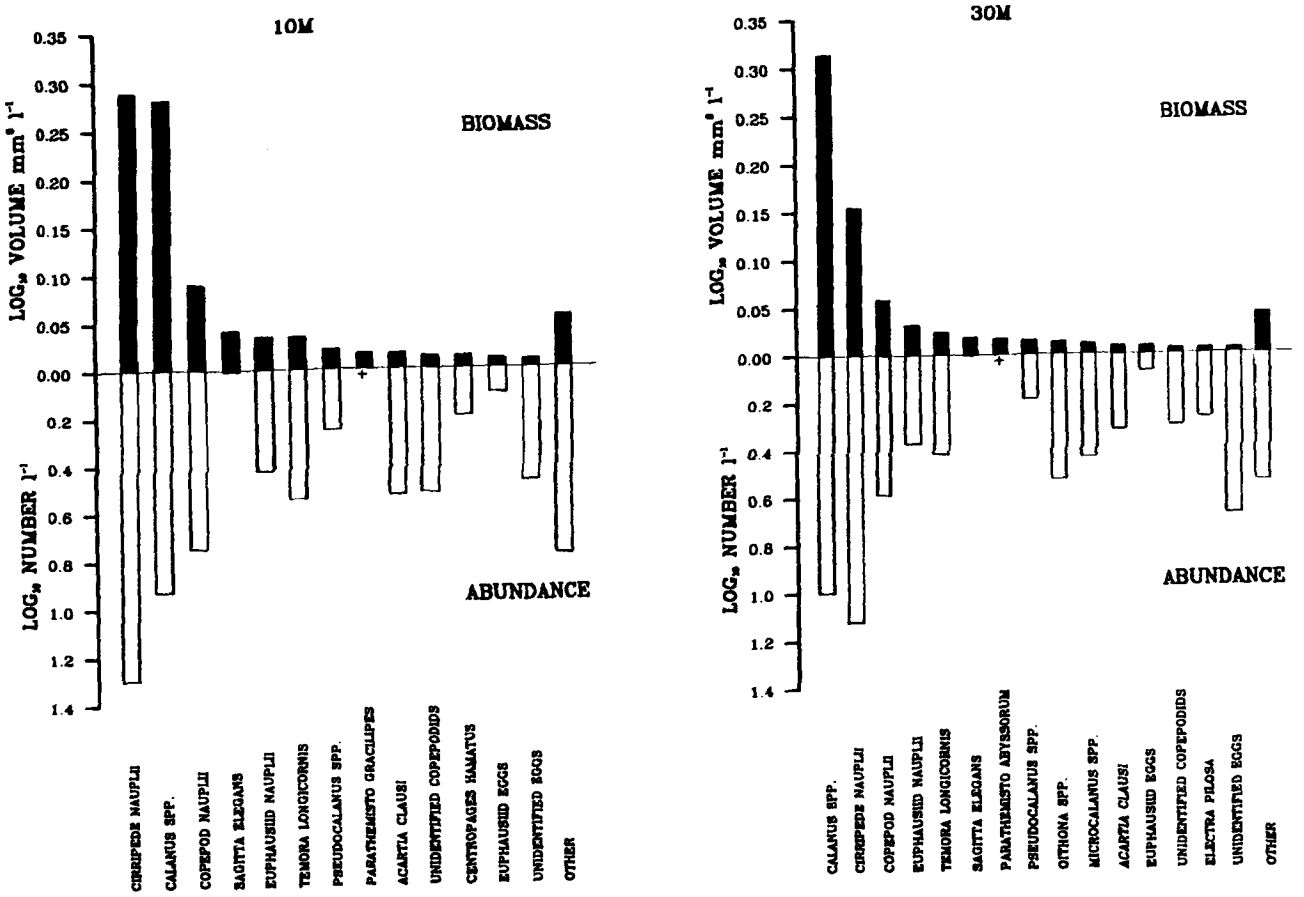


Figure 4.38 Total zooplankton biomass and abundance partitioned according to taxa for March 1987 at 10m and 30m. Only taxa which contributed to make up 95% of the total biomass are individually represented. The remaining taxa are collectively grouped as 'other'.

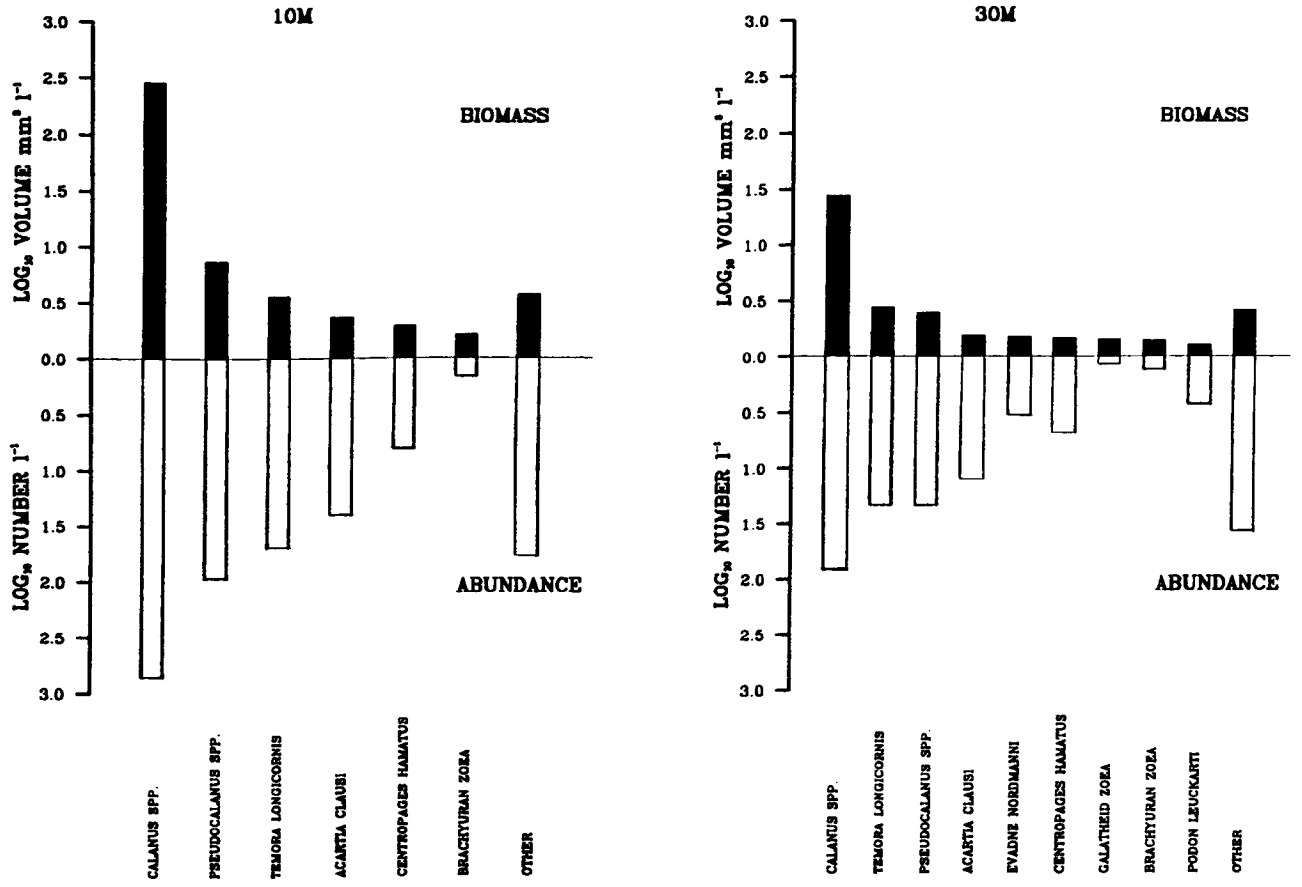


Figure 4.39 Total zooplankton biomass and abundance partitioned according to taxa for May 1986 at 10m and 30m. Only taxa which contributed to make up 99% of the total biomass are individually represented. The remaining taxa are collectively grouped as 'other'.

collected at 952 l^{-1}. Six taxa contributed 99% of the total biomass and all were copepods with the exception of brachyuran zoeae. Almost all of the biomass was made up by *Calanus* spp. which alone accounted for 95% of the estimated total. Of the remaining taxa, only *Pseudocalanus* spp. (90.86mm^3 l^{-1}) accounted for more than 1% of the total biomass.

At 30m the total biomass was lower at 30.4mm^3 l^{-1} as was the total number of animals at 176 l^{-1}. Most of the biomass still consisted of copepods with *Calanus* spp. accounting for 78% of the total with considerably smaller contributions from *Temora longicornis* and *Pseudocalanus* spp.. Two cladocerans, *Evadne nordmanni* and *Podon leuckartii,* and two types of decapod zoeae each contributed to 99% of the total biomass.

4.2.4.2 Biomass Partitioning Within Cruises

In this section biomass spectra are examined for each of the main station groups identified for each of the cruises using multivariate techniques. In each case the total spectrum representing the distribution of biomass for all taxa collected within the station group is given as well as individual spectra for those taxa which together accounted for 95% of the estimated total biovolume. Similarly arranged abundance spectra are also shown for each station group.

4.2.4.2.1 March 1987: 10m

Biomass spectra for each of the five main station groups identified from March at 10m depth are shown in Figure 4.40. Biomass is arranged in $\log_2$ size classes and the corresponding lengths in mm for each class are given in the figure caption. Abundance spectra are also shown for each station group. All estimates of total biovolume for each station group have been standardised by dividing the total biovolume by

Figure 4.40 Zooplankton size spectra by biomass, expressed as biovolume ($mm^3\ m^{-3}$), and abundance, expressed as (number m^{-3}), for stations comprising each of the groups identified using multivariate analyses at 10m, March 1987. Only taxa which contributed to make up 95% of the total biovolume are individually represented. The complete spectrum is represented by the 'Total'. Lengths (mm) corresponding to the $\log_2$ size classes shown in this figure are as follows: 6 = 0.064; 7 = 0.128; 8 = 0.256; 9 = 0.512; 10 = 1.024; 11 = 2.048; 12 = 4.096; 13 = 8.192; 14 = 16.384; 15 = 32.768. A list of abreviations for taxa included in this figure is given below.

CIR NAUP	= Cirripede nauplii
CALANUS	= *Calanus* spp.
COP NAUP	= Copepod nauplii
C.FIN	= *Calanus finmarchicus*
S.ELEG	= *Sagitta elegans*
EUPH NAUP	= Euphausiid nauplii
T.LONG	= *Temora longicornis*
PSCAL	= *Pseudocalanus* spp.
A.CLAUSI	= *Acartia clausi*
C.HAM	= *Centropages hamatus*
BRACHY	= Brachyuran zoeae
L.LITT	= *Littorina littorea*
OITHONA	= *Oithona* spp.
C.HEL	= *Calanus helgolandicus*
EUPH EGG	= Euphausiid egg
P.PARVUS	= *Paracalanus parvus*
MICROCAL	= *Microcalanus* spp.
CRUST EGG	= Crustacean egg
E.PILOSA	= *Electra pilosa*
UNID COP	= Unidentified copepodids
CYPRID	= Cirripede cyprid
POLY LARV	= Polychaete larvae
PAGURID	= Pagurid zoeae
SAGITTA	= *Sagitta* spp.
GAS LARV	= Gastropod larvae
CARID	= Caridean zoeae
P.GRACIL	= *Parathemisto gracilipes*

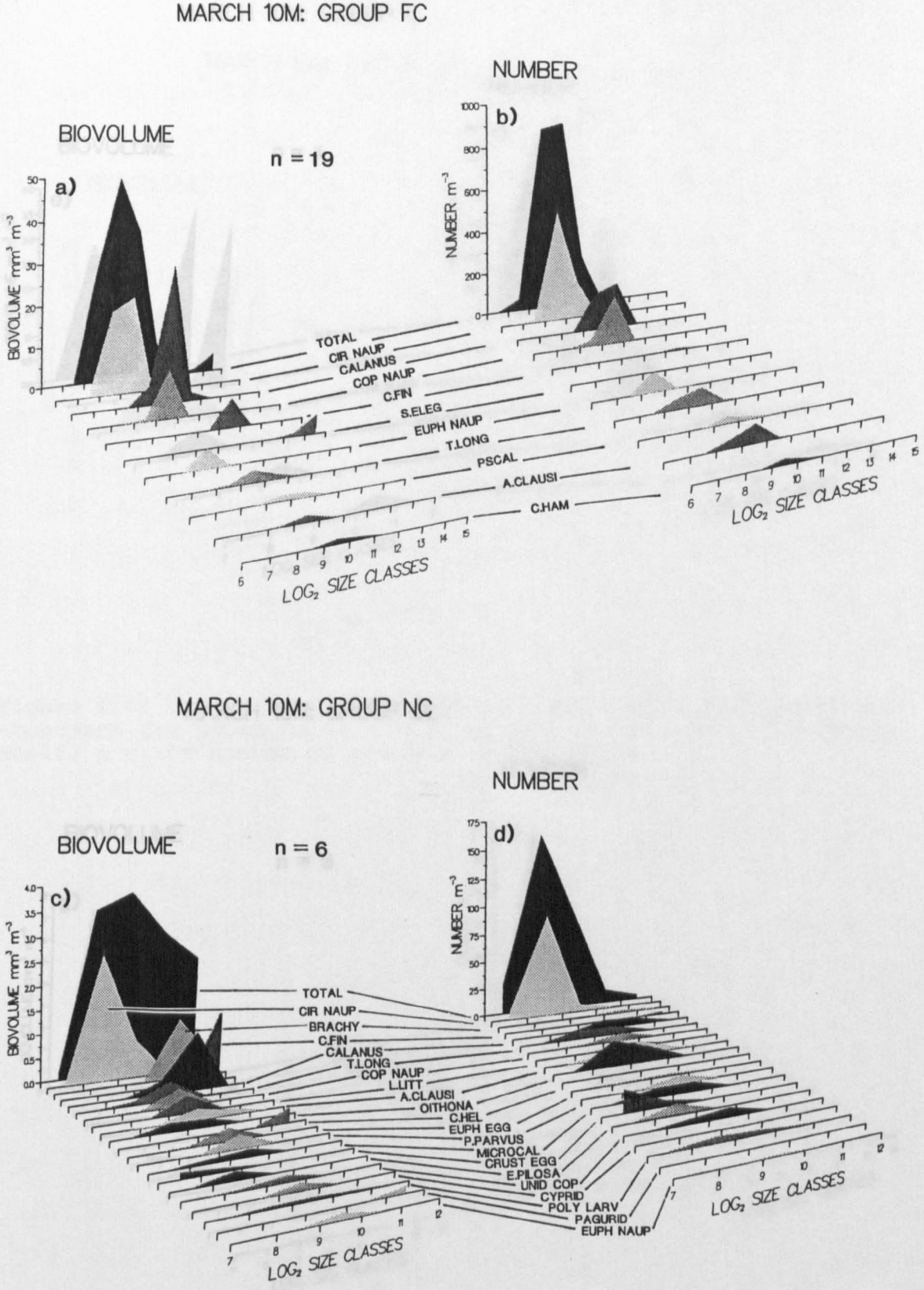


Figure 4.40 (Continued). Zooplankton size spectra by biomass and abundance for groups FC (a and b), and NC (c and d), at 10m, March 1987. FC = Firth of Clyde, NC = North Channel. n = the number of stations in each group.

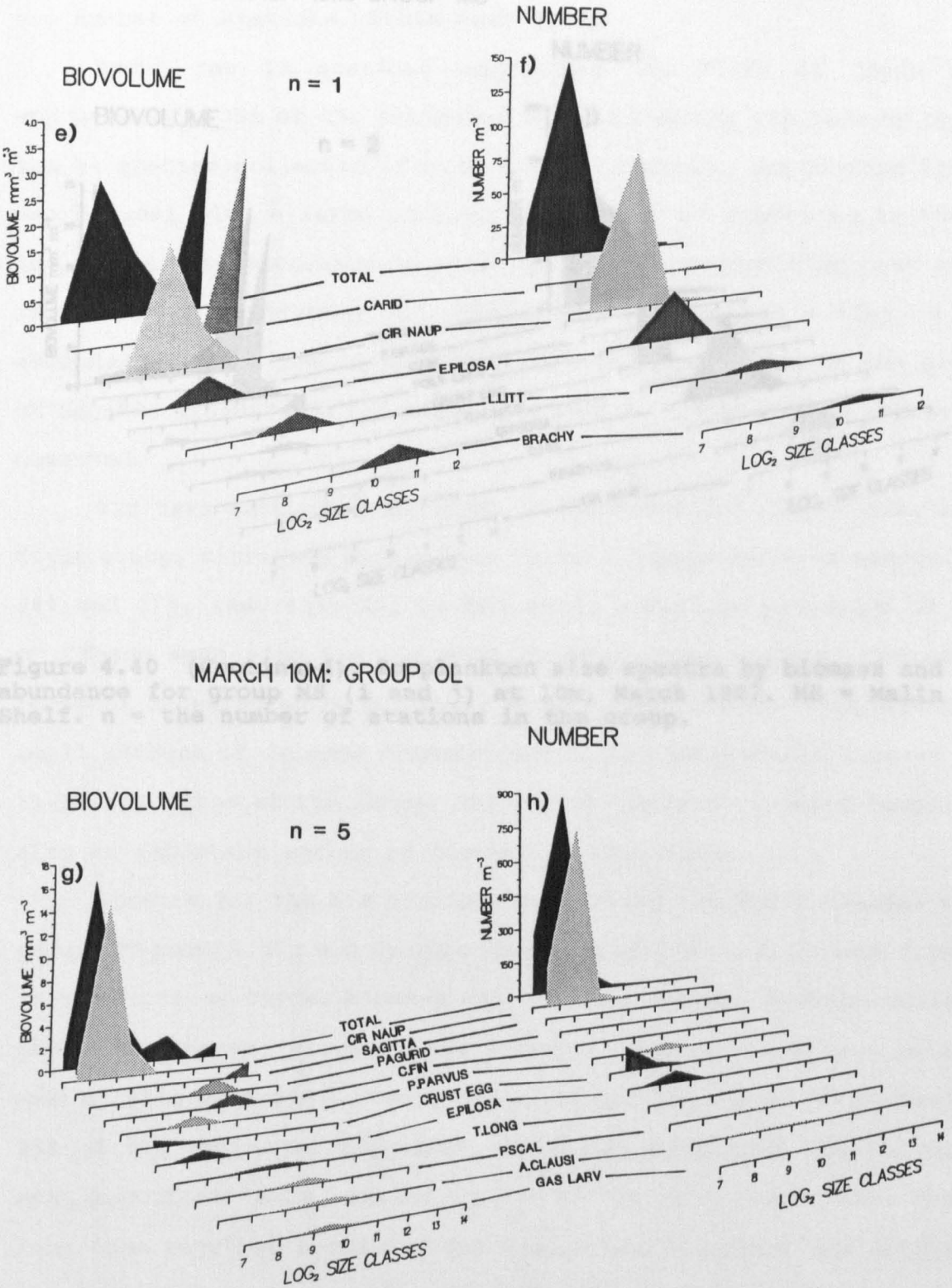


Figure 4.40 (Continued). Zooplankton size spectra by biomass and abundance for groups IL (e and f), and OL (g and h), at 10m, March 1987. IL= Inner Lorn OL = Outer Lorn. n = the number of stations in each group.

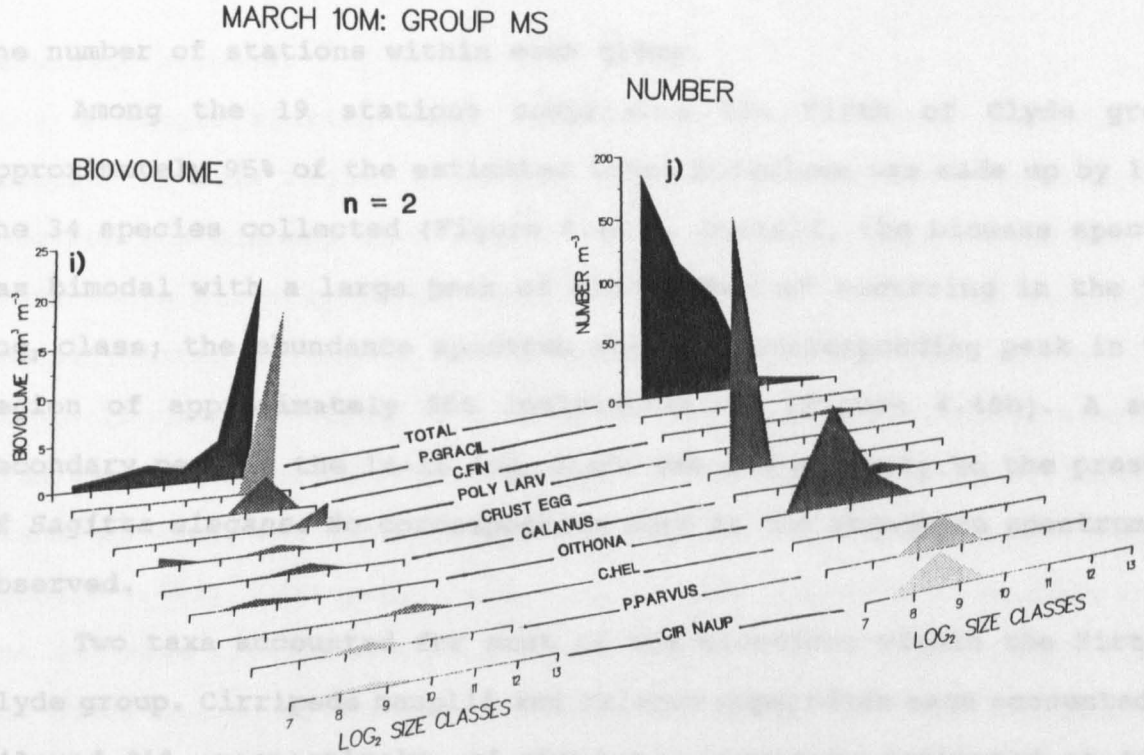


Figure 4.40 (Continued). Zooplankton size spectra by biomass and abundance for group MS (i and j) at 10m, March 1987. MS = Malin Shelf. n = the number of stations in the group.

the number of stations within each group.

Among the 19 stations comprising the Firth of Clyde group, approximately 95% of the estimated total biovolume was made up by 10 of the 34 species collected (Figure 4.40a). Overall, the biomass spectrum was bimodal with a large peak of about 50mm^3 m^{-3} occurring in the 9-10 $\log_2$ class; the abundance spectrum showed a corresponding peak in this region of approximately 900 individuals m^{-3} (Figure 4.40b). A small secondary peak in the 14-15 $\log_2$ class was due entirely to the presence of *Sagitta elegans*. No corresponding peak in the abundance spectrum was observed.

Two taxa accounted for most of the biovolume within the Firth of Clyde group. Cirripede nauplii and *Calanus* copepodids each accounted for 34% and 31%, respectively, of the total biovolume estimated at 130mm^3 m^{-3}. These were also the two most abundant taxa. Several medium-sized copepods contributed to the total biovolume in the 8-11 $\log_2$ classes and small numbers of *Calanus finmarchicus* contributed to the biomass in the 11-13 $\log_2$ class at the larger end of the spectrum. Copepod nauplii were also an important source of biomass at this time.

Spectra for the six stations comprising the North Channel station group (Figures 4.40c and d) were characteristically different from those in the Firth of Clyde. Biomass was distributed more homogeneously among the size classes, although the maximum value attained was only about 4mm^3 m^{-3} (Figure 4.40c). Twenty out of 33 species collected accounted for 95% of the estimated biovolume. Of these, cirripede nauplii were the most important taxon, making up 27% of the biovolume, while the first four taxa together accounted for 64%. Total biovolume was estimated at 13mm^3 m^{-3}. Cirripede nauplii were also the most important taxon in terms of overall abundance (Figure 4.40d). However, several large sized taxa which occurred in low numbers were important sources of biomass. These were brachyuran zoeae, *Calanus finmarchicus* and *Calanus* copepodids. Smaller copepods and meroplanktonic larvae comprised much of the

remaining biomass.

A single station comprised the Inner Lorn group and the size spectra for this region are shown in Figures 4.40e and f. The biomass spectrum was bimodal with a peak of 3mm^3 m^{-3} occurring in the 8-9 $\log_2$ class and a slightly larger peak of 3.5mm^3 m^{-3} in the 11-12 $\log_2$ class. Overall, total biomass in the Inner Lorn region was only 8mm^3 m^{-3}. Five of the 12 species collected made up 95% of the estimated total biovolume with the most important taxon being caridean zoeae (Figure 4.40e). This taxon, however, was not an important component in the abundance spectrum (Figure 4.40f). Cirripede nauplii were the main source of biomass in the smaller size classes and also accounted for the greatest proportion of the total number in the corresponding abundance spectrum. The remaining biomass was composed of meroplanktonic taxa which generally accounted for only a small proportion of both total biomass and number collected.

The biomass spectrum in the Outer Lorn group, containing five stations, was trimodal with a main peak of 17mm^3 m^{-3} in the 8-9 $\log_2$ class and two smaller peaks of 2.3 and 1.3mm^3 m^{-3} in the 11-12 and 13-14 $\log_2$ classes, respectively (Figure 4.40g). The total estimated biovolume for this station group was 28mm^3 m^{-3}. Eleven of a possible 29 species contributed to the overall size spectrum although cirripede nauplii alone accounted for 67% the total biovolume collected (Figure 4.40h). The second and third peaks in the biomass spectrum consisted of pagurid zoeae, and *Calanus finmarchicus* and *Sagitta* spp., respectively. None of these taxa made substantial contributions to the corresponding abundance spectrum.

The final group consisted of two stations located on the Malin Shelf. Here, the biomass spectrum was bimodal and the main proportion of the biovolume was contained in the larger size classes (Figure 4.40i). The total estimated biovolume for this station group was 33mm^3 m^{-3} and nine out of 22 taxa collected accounted for 95% of this value. Most of the biomass occurred in the larger size classes (11 to 13) and

was due to small numbers of *Parathemisto gracilipes*, with lesser contributions from *Calanus finmarchicus*, polychaete larvae, and *C. helgolandicus*. In the corresponding abundance spectrum, only *C. finmarchicus* made a noticeable contribution (Figure 4.40j). *Oithona* spp. and crustacean eggs both occurred at the smaller end of the spectrum and were important in terms of abundance. However, neither was of major importance in terms of estimated total biovolume. Overall, meroplanktonic taxa were of relatively less importance in terms of total biovolume and number collected than in any of the other station groups.

4.2.4.2.2 March 1987: 30m

Biomass spectra were examined for the four main station groups identified from samples collected in March at 30m (Figure 4.41). In the first group, containing 23 stations located in the Firth of Clyde and the North Channel, the total estimated biovolume was 80mm^3 m^{-3}. Of the 40 taxa collected, 14 made up 95% of the biovolume and the first three taxa, *Calanus* copepodids (42%), cirripede nauplii (15%) and *C. finmarchicus* (13%), together accounted for 70% of the overall total (Figure 4.41a). The shape of the biomass spectrum was bimodal with a peak of 30mm^3 m^{-3} in the 10-11 $\log_2$ size class due almost entirely to *Calanus* copepodids. A second smaller peak in the 13-14 $\log_2$ class resulted from small numbers of *Sagitta elegans*. Most of the remaining taxa, including small to medium-sized copepods and meroplankton, contributed to the 9-10 $\log_2$ class.

The abundance spectrum for the Firth of Clyde/North Channel station group was unimodal with peak abundance occurring in the 9-10 $\log_2$ class (Figure 4.41b). Many taxa contributed to the abundance spectrum in this region although not all are shown because they comprised only small amounts of the total biomass. Of the taxa shown, all occurred in this size class with the exception of *C. finmarchicus*

Figure 4.41 Zooplankton size spectra by biomass, expressed as biovolume (mm^3 m^{-3}), and abundance, expressed as (number m^{-3}), for stations comprising each of the groups identified using multivariate analyses at 30m, March 1987. Only taxa which contributed to make up 95% of the total biovolume are individually represented. The complete spectrum is represented by the 'Total'. Lengths (mm) corresponding to the log_2 size classes shown in this figure are as follows: 5 = 0.032; 6 = 0.064; 7 = 0.128; 8 = 0.256; 9 = 0.512; 10 = 1.024; 11 = 2.048; 12 = 4.096; 13 = 8.192; 14 = 16.384; 15 = 32.768. A list of abreviations for taxa included in this figure is given below.

CIR NAUP = Cirripede nauplii
CALANUS = *Calanus* spp.
COP NAUP = Copepod nauplii
C.FIN = *Calanus finmarchicus*
S.ELEG = *Sagitta elegans*
EUPH NAUP = Euphausiid nauplii
T.LONG = *Temora longicornis*
PSCAL = *Pseudocalanus* spp.
A.CLAUSI = *Acartia clausi*
C.HAM = *Centropages hamatus*
GALATH = Galatheid zoeae
L.LITT = *Littorina littorea*
OITHONA = *Oithona* spp.
C.HEL = *Calanus helgolandicus*
EUPH EGG = Euphausiid egg
P.PARVUS = *Paracalanus parvus*
MICROCAL = *Microcalanus* spp.
CRUST EGG = Crustacean egg
E.PILOSA = *Electra pilosa*
UNID COP = Unidentified copepodids
CYPRID = Cirripede cyprid
POLY LARV = Polychaete larvae
M.LUC = *Metridia lucens*
SAGITTA = *Sagitta* spp.
E.NORD = *Evadne nordmanni*
C.VANUS = *Ctenocalanus vanus*
P.ABYSS = *Parathemisto abyssorum*
E.ACUTA = *Euchaeta acuta*

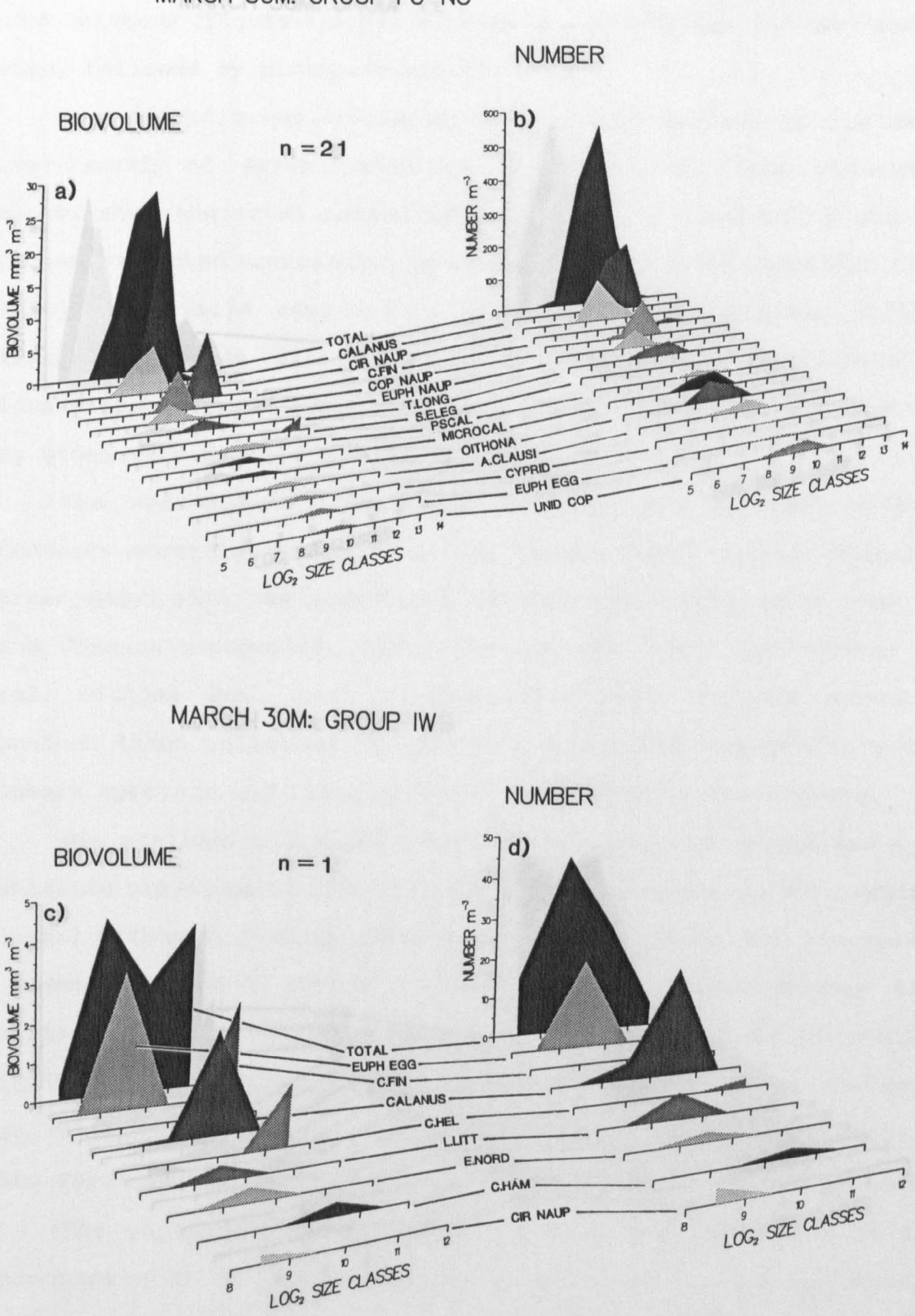


Figure 4.41 (Continued). Zooplankton size spectra by biomass and abundance for groups FC-NC (a and b), and IW (c and d), at 30m, March 1987. FC-NC = Firth of Clyde-North Channel, IW = Inchmarnock Water. n = the number of stations in each group.

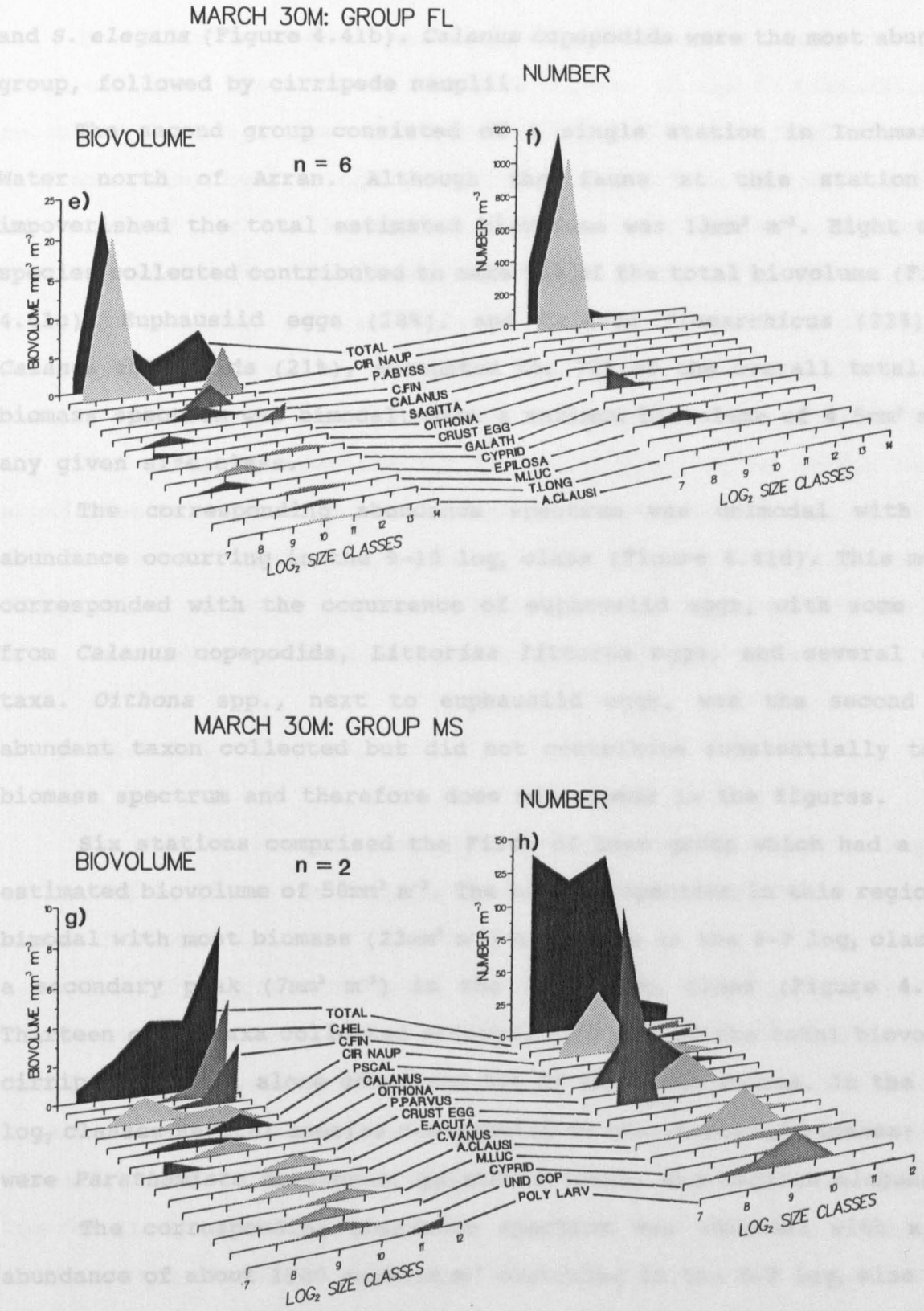


Figure 4.41 (Continued). Zooplankton size spectra by biomass and abundance for groups FL (e and f), and MS (g and h), at 30m, March 1987. FL = Firth of Lorn, MS = Main Shelf. n = the number of stations in each group.

and *S. elegans* (Figure 4.41b). *Calanus* copepodids were the most abundant group, followed by cirripede nauplii.

The second group consisted of a single station in Inchmarnock Water north of Arran. Although the fauna at this station was impoverished the total estimated biovolume was 13mm^3 m^{-3}. Eight of 13 species collected contributed to make 95% of the total biovolume (Figure 4.41c). Euphausiid eggs (28%), and *Calanus finmarchicus* (23%) and *Calanus* copepodids (21%), accounted for 72% of the overall total. The biomass spectrum was bimodal, with a maximum biovolume of 4.5mm^3 m^{-3} in any given size class.

The corresponding abundance spectrum was unimodal with peak abundance occurring in the 9-10 $\log_2$ class (Figure 4.41d). This mostly corresponded with the occurrence of euphausiid eggs, with some input from *Calanus* copepodids, *Littorina littorea* eggs, and several other taxa. *Oithona* spp., next to euphausiid eggs, was the second most abundant taxon collected but did not contribute substantially to the biomass spectrum and therefore does not appear in the figures.

Six stations comprised the Firth of Lorn group which had a total estimated biovolume of 50mm^3 m^{-3}. The biomass spectrum in this region was bimodal with most biomass (23mm^3 m^{-3}) occurring in the 8-9 $\log_2$ class and a secondary peak (7mm^3 m^{-3}) in the 12-13 $\log_2$ class (Figure 4.41e). Thirteen of 32 taxa collected accounted for 95% of the total biovolume; cirripede nauplii alone comprised 53% of the total volume. In the 12-14 $\log_2$ classes several species contributed to the increased biomass; these were *Parathemisto abyssorum*, galatheid zoeae, and *Sagitta elegans*.

The corresponding abundance spectrum was unimodal with a peak abundance of about 1200 animals m^{-3} occurring in the 8-9 $\log_2$ size class (Figure 4.41f). Cirripede nauplii were the only group to contribute substantially to the abundance spectrum in the Firth of Lorn group. None of the species comprising the secondary peak in the biomass spectrum contributed noticeably to the abundance spectrum.

The Malin Shelf group was again composed of two stations, with a total estimated biovolume of 20mm^3 m^{-3}. Fifteen of the 27 taxa collected accounted for 95% of the total biovolume with *Calanus helgolandicus* and *C. finmarchicus* comprising 30% and 18%, respectively (Figure 4.41g). As was observed for the Malin Shelf at 10m, the greatest biomass was distributed towards the larger end of the spectrum in the 11-12 $\log_2$ class. Otherwise, progressively smaller amounts of biomass were contributed by the medium and small size classes. Biomass within these smaller size classes was quite evenly distributed across the spectrum.

The abundance spectrum for the Malin Shelf group showed highest abundances in the smaller size classes which contributed only marginally to the total biomass (Figure 4.42h). *C. helgolandicus* and *C. finmarchicus* occurred in relatively low numbers but, due to their large size, were important contributors to the total biovolume.

4.2.4.2.3 May 1986: 10m

The multivariate analyses identified five main groups in May 1986 at 10m depth. Biomass and abundance spectra for each of these groups are shown in Figure 4.42.

The first group consisted of a single station in Loch Fyne. The total estimated biovolume at this station was high, at 3 x 10^5 mm^{3}m^{-3}. Out of 15 taxa collected only *Calanus*, i.e. copepodids and adult *C. finmarchicus*, contributed to the biomass spectrum; copepodids comprised 92% and adults 4% of the total biovolume, respectively (Figure 4.42a). The resulting spectrum was unimodal with most biomass being concentrated in the larger size classes. *Calanus* copepodids were also numerically the most abundant taxon (Figure 4.42b) while taxa occurring in the smaller size classes (i.e. < 10) contributed only marginally to the corresponding biomass spectrum (Figure 4.42a).

The biomass spectrum for the Arran Deep group was also

Figure 4.42 Zooplankton size spectra by biomass, expressed as biovolume (mm^3 m^{-3}), and abundance, expressed as (number m^{-3}), for stations comprising each of the groups identified using multivariate analyses at 10m, May 1986. Only taxa which contributed to make up 95% of the total biovolume are individually represented. The complete spectrum is represented by the 'Total'. Lengths (mm) corresponding to the $\log_2$ size classes shown in this figure are as follows: 4 = 0.016; 5 = 0.032; 6 = 0.064; 7 = 0.128; 8 = 0.256; 9 = 0.512; 10 = 1.024; 11 = 2.048; 12 = 4.096; 13 = 8.192; 14 = 16.384. A list of abreviations for taxa included in this figure is given below.

CIR NAUP	= Cirripede nauplii
CALANUS	= *Calanus* spp.
COP NAUP	= Copepod nauplii
C.FIN	= *Calanus finmarchicus*
E.NORD	= *Evadne nordmani*
GALATH	= Galatheid zoeae
T.LONG	= *Temora longicornis*
PSCAL	= *Pseudocalanus* spp.
A.CLAUSI	= *Acartia clausi*
C.HAM	= *Centropages hamatus*
BRACHY	= Brachyuran zoeae
P.LEUCK	= *Podon leuckartii*
OITHONA	= *Oithona* spp.
C.HEL	= *Calanus helgolandicus*
T.HELGO	= *Tomopteris helgolandica*
C.TYP	= *Centropages typicus*
M.LUC	= *Metridia lucens*
UNID COP	= Unidentified copepodids
CYPRID	= Cirripede cyprid
PAGURID	= Pagurid zoeae

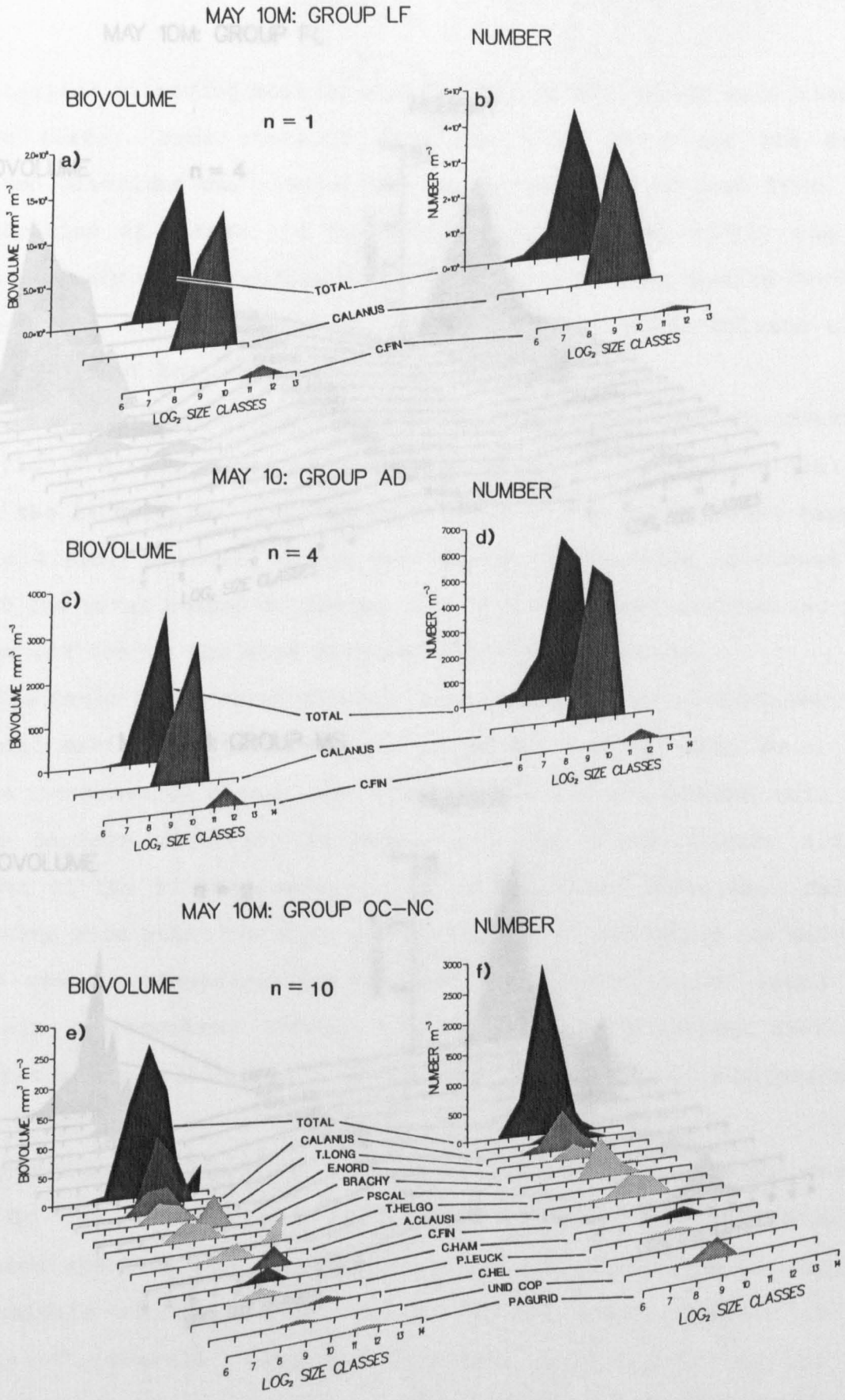


Figure 4.42 (Continued). Zooplankton size spectra by biomass and abundance for groups LF (a and b), AD (c and d), and OC-NC (e and f), at 10m, May 1986. LF = Loch Fyne, AD = Arran Deep, OC-NC Outer Clyde-North Channel. n = the number of stations in each group.

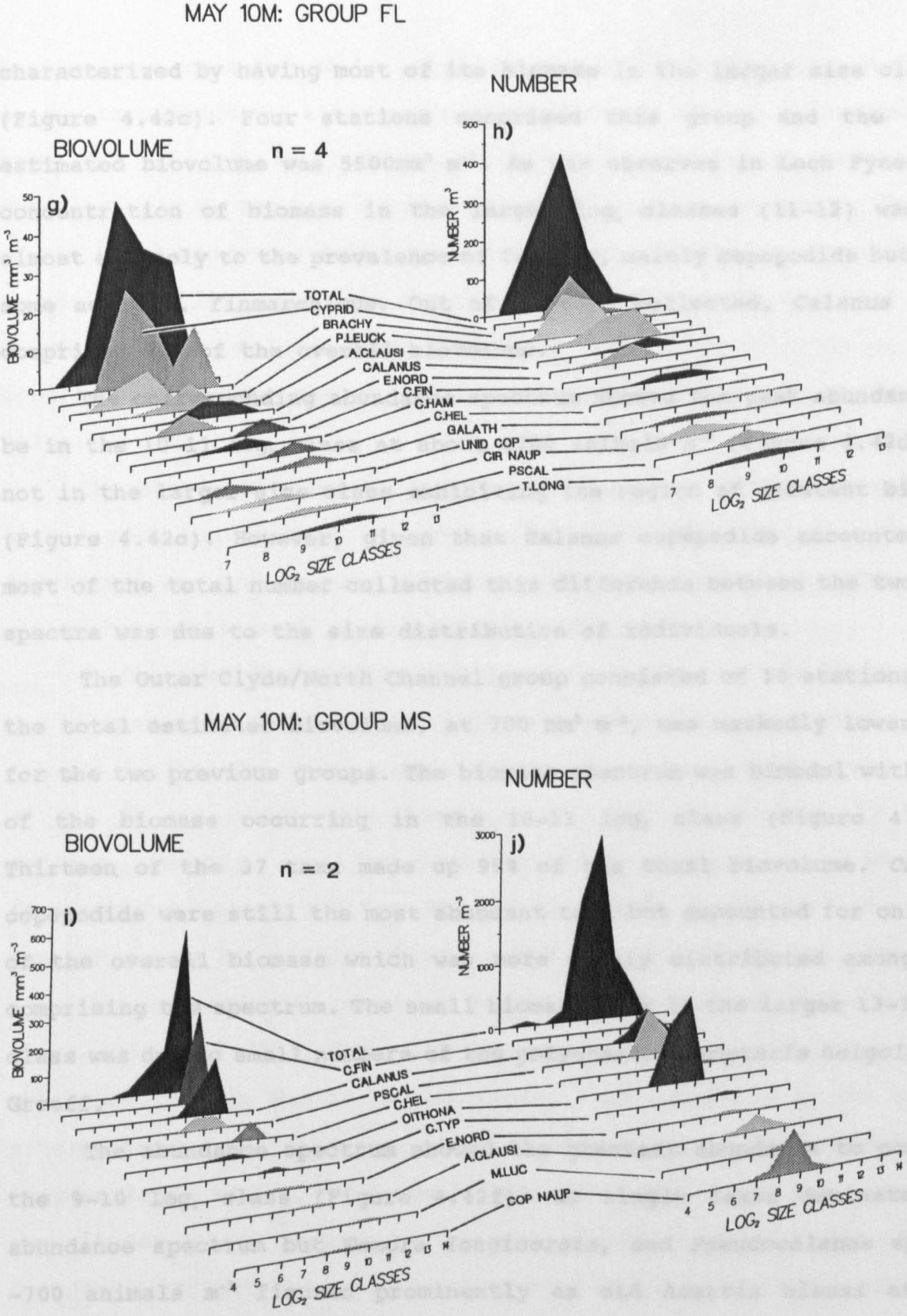


Figure 4.42 (Continued). Zooplankton size spectra by biomass and abundance for groups FL (g and h), and MS (i and j), at 10m, May 1986. FL = Firth of Lorn, MS = Malin Shelf. n = the number of stations in each group.

characterized by having most of its biomass in the larger size classes (Figure 4.42c). Four stations comprised this group and the total estimated biovolume was 5500mm^3 m^{-3}. As was observed in Loch Fyne, the concentration of biomass in the larger $\log_2$ classes (11-12) was due almost entirely to the prevalence of *Calanus*, mainly copepodids but also some adult *C. finmarchicus*. Out of 20 taxa collected, *Calanus* alone comprised 96% of the overall biovolume.

The corresponding abundance spectrum showed the peak abundance to be in the 10-11 $\log_2$ class at about 6700 animals m^{-3} (Figure 4.42d) and not in the larger size class exhibiting the region of greatest biomass (Figure 4.42c). However, given that *Calanus* copepodids accounted for most of the total number collected this difference between the two size spectra was due to the size distribution of individuals.

The Outer Clyde/North Channel group consisted of 10 stations, and the total estimated biovolume, at 700 mm^3 m^{-3}, was markedly lower than for the two previous groups. The biomass spectrum was bimodal with most of the biomass occurring in the 10-11 $\log_2$ class (Figure 4.42e). Thirteen of the 37 taxa made up 95% of the total biovolume. *Calanus* copepodids were still the most abundant taxa but accounted for only 30% of the overall biomass which was more evenly distributed among taxa comprising the spectrum. The small biomass peak in the larger 13-14 $\log_2$ class was due to small numbers of the polychaete *Tomopteris helgolandica* Greeff.

The abundance spectrum showed the greatest abundance to occur in the 9-10 $\log_2$ class (Figure 4.42f). No single taxon dominated the abundance spectrum but *Temora longicornis*, and *Pseudocalanus* spp. at ~700 animals m^{-3} figured prominently as did *Acartia clausi* at ~350 animals m^{-3}. Overall, both the abundance and biomass spectra were composed of similar contributions from a number of different taxa.

Four stations comprised the Firth of Lorn group for which the biomass spectrum is shown in Figure 4.42g. Total biovolume at this

station was estimated to be 125mm^3 m^{-3} and this was distributed fairly evenly throughout the size spectrum. Fourteen of 36 taxa contributed to make 95% of the total biovolume. Meroplankton still contributed substantially to the overall spectrum, with cyprids accounting for 34% of the total biovolume followed by brachyuran zoeae which accounted for an additional 15%. Galatheid zoeae and cirripede nauplii were also among the top 14 taxa. *Calanus* copepodids ranked only fifth in terms of their contribution to the total biovolume, accounting for only 7% of the total value.

The abundance spectrum for the Firth of Lorn group was unimodal with a peak in the 9-10 $\log_2$ class (Figure 4.42h). Cyprids and *Podon leuckartii* at ~100 animals m^{-3} were most abundant in this size class although several other species also contributed.

In the final group, consisting of two stations on the Malin Shelf, the biomass spectrum showed most biomass among the larger size classes (Figure 4.42i). The total estimated biovolume for this area was 900mm^3 m^{-3} and 10 out of 28 taxa accounted for 95% of the overall total. *Calanus*, roughly equal proportions of copepodids and adult *C. finmarchicus*, accounted for 69% of the total biovolume. The eight remaining taxa had little effect on the shape of the overall spectrum.

The corresponding abundance spectrum showed a peak in the 9-10 $\log_2$ class (Figure 4.42j). This did not correspond with the biomass peak which occurred in the 11-12 $\log_2$ class. Peak abundance in the smaller size class was due to large numbers of *Oithona* spp. (~1200 animals m^{-3}), *Pseudocalanus* spp. (~700 animals m^{-3}), and several other taxa which contributed lesser amounts to the total number. None of these taxa was a major contributor to the biomass spectrum due to their relatively small size. Similarly, *Calanus* adults and copepodids comprised only a small fraction of the abundance spectrum while *Calanus* copepodids were ranked second and accounted for 32%.

4.2.4.2.4 May 1986: 30m

Biomass and abundance spectra are shown in Figure 4.43. for the four groups identified in May at 30m, using multivariate statistics. The first group, designated Arran Deep, contained five stations and had a total estimated biovolume of 5000 mm^3 m^{-3}. Most of the biomass within this group was concentrated in the larger size classes (Figure 4.43a). Although 28 taxa were collected overall, *Calanus* alone accounted for 95% of the total biovolume; copepodids comprised 81% and adult *C.finmarchicus* 14%. *C.finmarchicus* occurred only in the 11-12 log_2 class while the copepodids covered a range of classes from 9-12.

In the abundance spectrum *Calanus* copepodids also accounted for most of the total number collected with a smaller contribution from the adults (Figure 4.43b). Smaller taxa occurring in the 7-9 log_2 class range of the abundance spectrum did not contribute sufficiently large amounts to the biovolume to be included in the biomass spectrum.

The biomass and abundance spectra for the Mixed Zone group (Figures 4.43c and d) were quite different from those observed in the Arran Deep (Figures 4.43a and b). The total estimated biovolume for this group, consisting of 11 stations, was lower at ~700mm^3 m^{-3} and, in general, the biomass was fairly evenly distributed among those taxa contributing to the spectrum. Sixteen out of 45 taxa accounted for 95% of the total biovolume. *Calanus* spp. was the most abundant taxon and comprised 23% of the total, although *Temora longicornis* and *Pseudocalanus* spp. each accounted for 21% and 14% of the total biovolume, respectively. Meroplankton, notably decapod zoeae, were still fairly important in terms of biomass, and comprised most of the biomass in the larger size classes.

The corresponding abundance spectrum showed a sharp peak in the 9-10 log_2 class of about 4000 animals m^{-3} (Figure 4.43d). No single taxon accounted for this peak in abundance, although *T. longicornis* and

Figure 4.43 Zooplankton size spectra by biomass, expressed as biovolume ($mm^3\ m^{-3}$), and abundance, expressed as (number m^{-3}), for stations comprising each of the groups identified using multivariate analyses at 30m, May 1986. Only taxa which contributed to make up 95% of the total biovolume are individually represented. The complete spectrum is represented by the 'Total'. Lengths (mm) corresponding to the $\log_2$ size classes shown in this figure are as follows: 4 = 0.016; 5 = 0.032; 6 = 0.064; 7 = 0.128; 8 = 0.256; 9 = 0.512; 10 = 1.024; 11 = 2.048; 12 = 4.096; 13 = 8.192; 14 = 16.384. A list of abreviations for taxa included in this figure is given below.

CIR NAUP	= Cirripede nauplii
CALANUS	= *Calanus* spp.
COP NAUP	= Copepod nauplii
C.FIN	= *Calanus finmarchicus*
S.ELEG	= *Sagitta elegans*
E.NORD	= *Evadne nordmanni*
T.LONG	= *Temora longicornis*
PSCAL	= *Pseudocalanus* spp.
A.CLAUSI	= *Acartia clausi*
C.HAM	= *Centropages hamatus*
BRACHY	= Brachyuran zoeae
P.LEUCK	= *Podon leuckartii*
OITHONA	= *Oithona* spp.
C.HEL	= *Calanus helgolandicus*
T.HELG	= *Tomopteris helgolandica*
P.PARVUS	= *Paracalanus parvus*
GALATH	= Galatheid zoeae
M.LUC	= *Metridia lucens*
UNID COP	= Unidentified copepodids
CYPRID	= Cirripede cyprid
PAGURID	= Pagurid zoeae
CARID	= Caridean zoeae

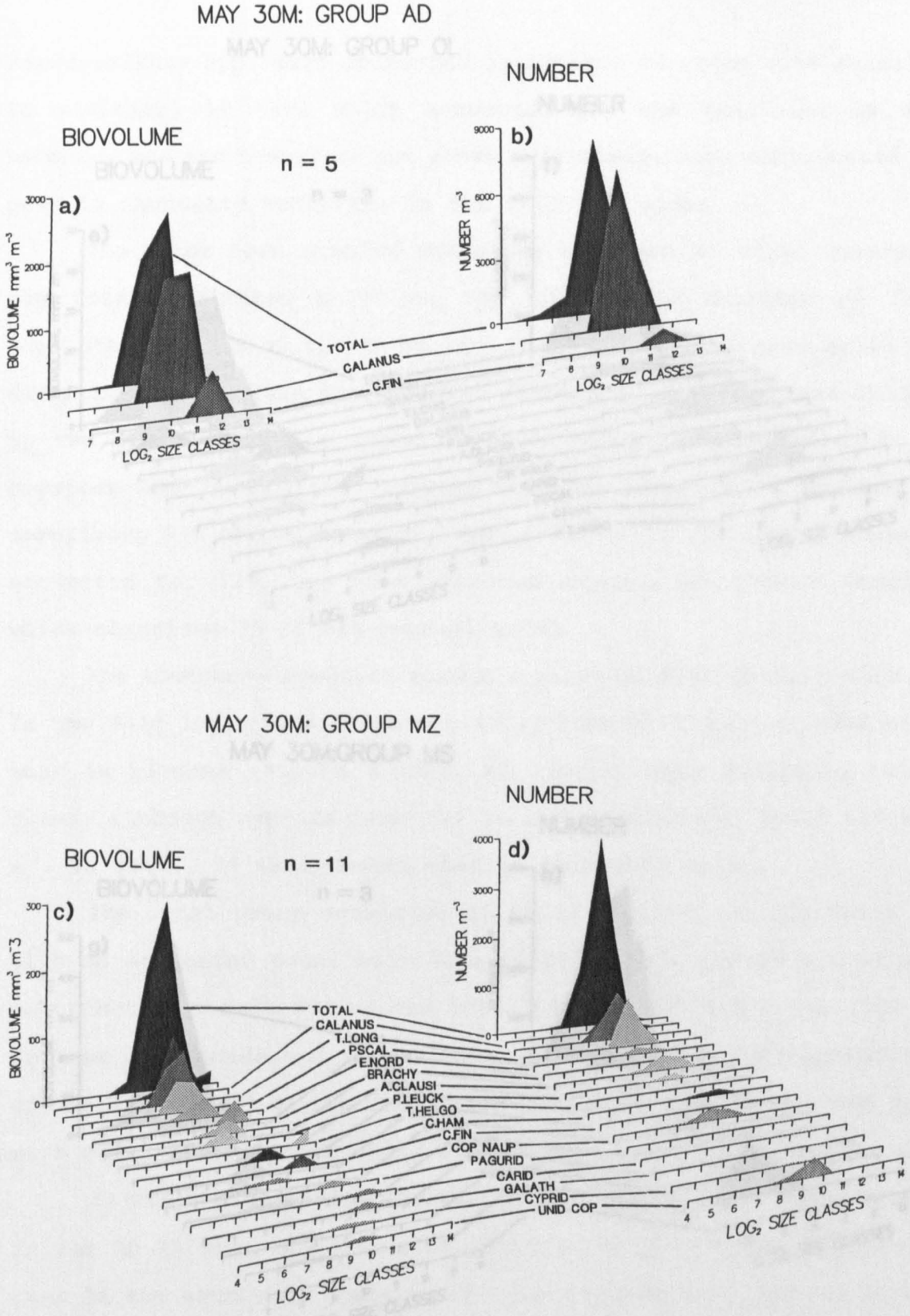


Figure 4.43 (Continued). Zooplankton size spectra by biomass and abundance for groups AD (a and b), and MZ (c and d), at 30m, May 1986. AD = Arran Deep, MZ = Mixed Zone. n = the number of stations in each group.

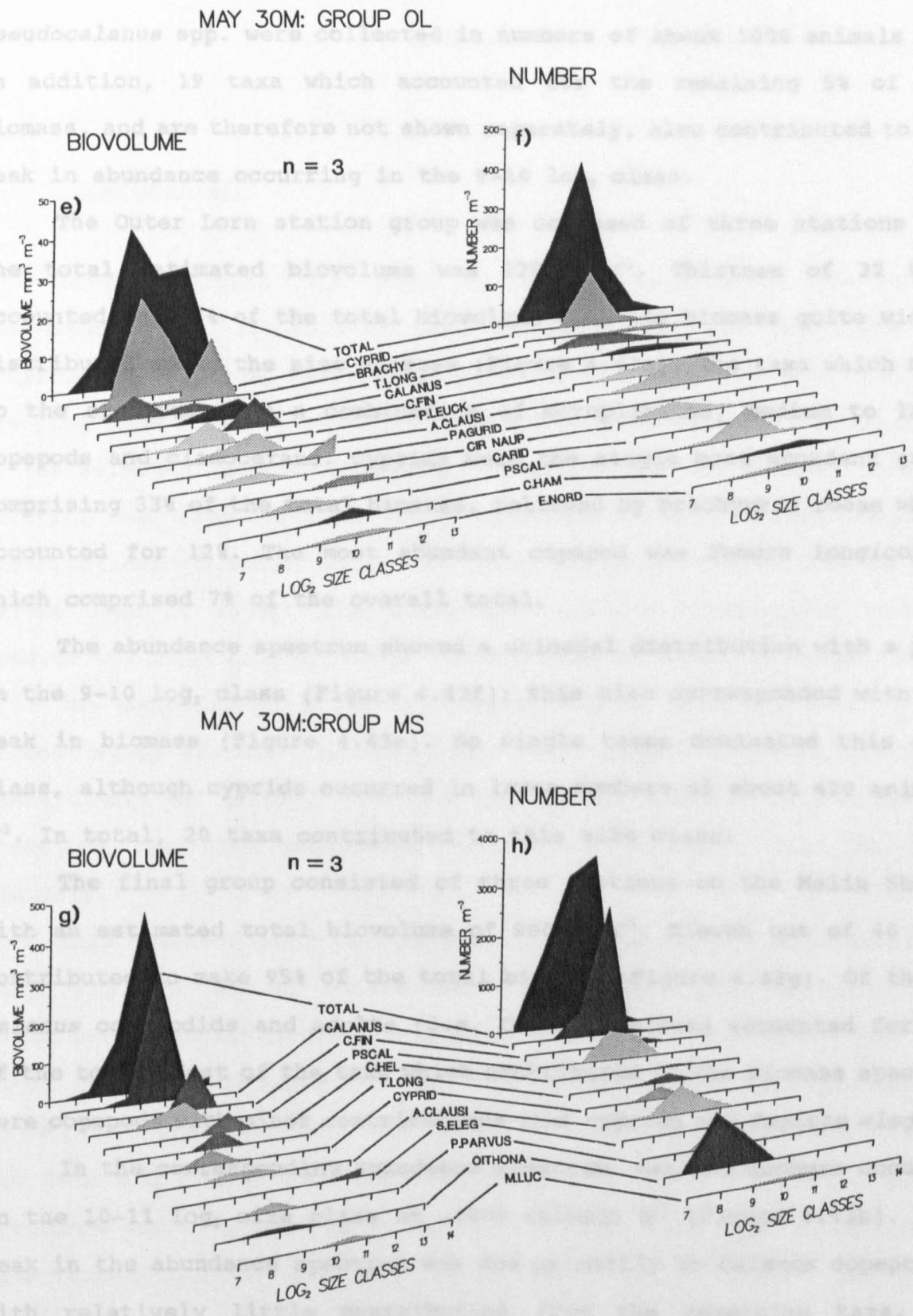


Figure 4.43 (Continued). Zooplankton size spectra by biomass and abundance for groups OL (e and f), and MS (g and h), at 30m, May 1986. OL = Outer Lorn, MS = Malin Shelf. n = the number of stations in each group.

Pseudocalanus spp. were collected in numbers of about 1000 animals m^{-3}. In addition, 19 taxa which accounted for the remaining 5% of the biomass, and are therefore not shown separately, also contributed to the peak in abundance occurring in the 9-10 log_2 class.

The Outer Lorn station group was composed of three stations and the total estimated biovolume was 120mm^3 m^{-3}. Thirteen of 32 taxa accounted for 95% of the total biovolume with the biomass quite widely distributed among the size classes (Figure 4.43e). The taxa which made up the spectrum were a combination of meroplankton, medium to large copepods and cladocerans. Cyprids were the single most abundant group comprising 33% of the total biomass, followed by brachyuran zoeae which accounted for 12%. The most abundant copepod was *Temora longicornis* which comprised 7% of the overall total.

The abundance spectrum showed a unimodal distribution with a peak in the 9-10 log_2 class (Figure 4.43f); this also corresponded with the peak in biomass (Figure 4.43e). No single taxon dominated this size class, although cyprids occurred in large numbers of about 420 animals m^{-3}. In total, 20 taxa contributed to this size class.

The final group consisted of three stations on the Malin Shelf, with an estimated total biovolume of 900mm^3 m^{-3}. Eleven out of 40 taxa contributed to make 95% of the total biomass (Figure 4.43g). Of these, *Calanus* copepodids and adults (i.e. *C.finmarchicus)* accounted for 61% of the total. Most of the taxa which contributed to the biomass spectrum were copepods with minor contributions from cyprids and *Sagitta elegans*.

In the corresponding abundance spectrum, maximum numbers occurred in the 10-11 log_2 size class at ~3600 animals m^{-3} (Figure 4.43h). This peak in the abundance spectrum was due primarily to *Calanus* copepodids with relatively little contribution from the remaining taxa. One exception was *Oithona* spp., which was fairly abundant in the 8-10 log_2 classes, but which was not an important component of the total biovolume due to its small size.

5. DISCUSSION

5.1 IMAGE ANALYSIS

Image analysis was used in the present study to obtain measurements for zooplankton taxa examined from the March and May cruises. In addition, several experiments were conducted when devising the programme in order to select a length measurement, and the accuracy of the selected function for several copepod taxa and possible sources of error were also examined. Other experiments examined size frequency distributions generated using the image analyser, variability in grey values used in object discrimination, and the relationship between prosome and total body projected surface area for selected copepod taxa.

The experiment to select a length measurement for use in the present study was not conducted with the intention of assessing length measurements in general, but the results do raise some interesting questions regarding measurement parameters routinely used in image analysis.

Data obtained using all three length measurements available on the image analyser showed considerable variability when compared with measurements obtained using a microscope at 50X; the MOMENT and DMAX functions gave consistently higher values, while the FERET measurement showed no overall pattern. The nature of the variability observed for the DMAX and MOMENT functions suggests that factors relating to the programme and/or practical set-up used in the study contributed to the measurement error. Although this would also affect the FERET measurement, the random nature of the variability suggests it was also partly due to the measurement algorithm. FERET measurements are sensitive to object orientation (Joyce-Loebl 1985), whereas the MOMENT and DMAX functions are not (Kontron 1985). It is probable that this

contributed to the greater error associated with the FERET measurements.

Previous studies involving image analysis have often used FERET measurements as estimates of length (e.g. Dietrich and Uhlig 1984; Rolke and Lenz 1984; Estep *et al.* 1986; Estep and MacIntyre 1989). Other studies merely refer to cell length (e.g. Furuya 1982; Tsuji and Nishikawa 1984) or longest dimension (e.g. Gorsky *et al.* 1989). These terms are ambiguous as they do not indicate the exact nature of the measurement with respect to orientation or the number of projections used.

Data regarding the accuracy of image analysis measurements versus microscope measurements are available from several studies (Furuya 1982; Tsuji and Nishikawa 1984; Estep *et al.* 1986; Gorsky *et al.* 1989) although the nature of the comparisons varies. Gorsky *et al.* (1989) provided data comparing length measurements (the longest dimension) for four algal species made using an image analyser, a microscope at 335X, and photographic enlargements of the algae and stage micrometer. The image analyser values deviated from the corresponding microscope measurements by as much as +23% to -8.5%; however, the microscope measurements themselves deviated from the photographic enlargements, emphasising the effect of magnification. Estep *et al.* (1986) used fluorescent spheres ranging in size from 0.21 to 1.73µm to check the accuracy of their system in measuring cell diameters and areas. For all sizes, with the exception of 0.21µm, near the lower limit of resolution, measurements made with the image analyser were within 6% of the manufacturer's specifications. However, cell diameters and areas for the 0.21µm sphere were overestimated by 24% and 84% respectively. This resulted in a corresponding overestimate in biovolume of 118% (Estep *et al.* 1986). Tsuji and Nishikawa (1984) found good agreement between cell lengths of the dinoflagellate *Prorocentrum triestinum* measured by hand and using the image analyser, while Furuya (1982) found no significant difference in mean cell lengths for four species of phytoplankton

measured using an image analysis system and by hand.

These studies all serve to illustrate the variability which can occur when making length measurements. In the studies cited above, length comparisons have been made for phytoplankton cells which have relatively simple morphometric shapes and all comparisons have been based on mean values. The results of this study have shown, using paired measurements, that considerable variability can occur at the individual level, particularly in the FERET measurements. This needs to be borne in mind when choosing a length measurement, and studies to determine the cumulative effect this may have on estimates of biovolume are required. It is probable that, in general, greater variability will be observed for zooplankton than for phytoplankton, given their greater morphometric complexity.

The results of the experiment to examine the effects of magnification on measurements made using the MOMENT function suggested that the variability observed could not be attributed to the different magnification levels. Measurements made using the microscope at 12X, a lower magnification than used for the image analyser (15X) in the present study, showed no significant difference from measurements made at 50X. However, the fact that length measurements for *Oithona* spp. and *Pseudocalanus* spp. were significantly different from the corresponding microscope measurements, but measurements for *Calanus finmarchicus* were not, suggests that magnification within the image analysis system itself may have contributed to the error.

The accuracy of the image analyser will be greatly affected by the resolution of the system. In the present study, the area covered by each square pixel at 15X was approximately $4 \times 10^{-4} mm^2$. The minimum area measured for individuals of *Oithona* spp., *Pseudocalanus* spp., and *Calanus finmarchicus* in each of the cruises is summarised in Table 5.1. Clearly, for *Oithona* spp. the accuracy of the measurements for some of the smaller individuals was limited by the resolution of the image. It

Table 5.1 Minimum areas (AR) recorded using the image analyser and the corresponding number of pixels (PX) for *Oithona* spp., *Pseudocalanus* spp., and *Calanus finmarchicus* collected at 10 and 30m in March 1987 and May 1986. All areas are in mm^2.

Taxa	March 10m		March 30m		May 10m		May 30m	
	AR	PX	AR	PX	AR	PX	AR	PX
Oithona spp.	.0317	77	.0226	55	.0067	16	.001	2
Pseudocalanus spp.	.1012	245	.0833	201	.0599	145	.0456	110
Calanus finmarchicus	1.194	2962	1.223	3034	.9944	2467	.884	2193

is unlikely that this was a problem for more than a small number of individuals occurring in the May cruise at 30m, the remaining individuals all being above the minimum values listed in Table 5.1.

There are several other potential sources of error which could have contributed to the observed variability in length measurements. The fact that length and area were measured only for the prosome required the use of eroding and dilating functions in order to remove appendages, antennae and the urosome. Incomplete removal of these body parts may have resulted in overestimates of prosome length. Probably of greater importance is the fact that zooplankton were immersed in a thin layer of filtered seawater when measured by the image analyser, which was not taken into account when the scale was entered for calibration. This may have affected the accuracy of the measurements and contributed to the consistently higher values obtained. This factor should be taken into account prior to any future use of the programme.

It is interesting to note, however, that length frequency data collected for *Calanus* spp. did not differ significantly from that obtained using the microscope at 50X magnification. Measurements used in this comparison were not paired so the degree of variability in individual measurements is unknown. Jeffries *et al.* (1980) also found no statistical difference between length frequency distributions for 300

Calanus, stages C4 to C6, obtained using an image analyser and a microscope at 12X. In the present study, it is probable that the comparable results were due to the relatively large size of *Calanus* individuals. If the experiment had been repeated using a smaller sized species the results may have been quite different.

The results of the experiment examining variability in grey values for different copepod taxa also raise some interesting questions regarding the use of fully automated programmes. Initial attempts to set global discrimination levels in the present study were unsuccessful. Different taxa, and even individuals within taxa, often showed widely variable grey values such that grey levels which optimally discriminated some individuals were less than optimal for others. This problem appeared partially related to size: in the present study, therefore different routines within the image analysis programme were developed to compensate for this variability.

The grey values used to discriminate the three copepod taxa examined in the present study showed considerable variability. This could be related to factors such as nutritional status and developmental stage. Use of a fully automated programme may therefore encounter problems in equally discriminating individual organisms within a mixed plankton sample. The effect this could have on individual biovolume measurements is unknown.

Eisma *et al.* (1990) preset parameters including shading correction and discrimination levels before processing negatives taken by underwater cameras to examine particle flocs, though they recognised that apparent differences in size could occur if threshold values were incorrectly set. Necessary adjustments, due to negatives exposed or developed under differing conditions, were achieved manually by an operator who compared processed and original images and adjusted threshold levels until the sizes corresponded. This illustrates the continued importance of an operator to assess the accuracy of the

measurements being made and to intervene when necessary.

The relationship between projected surface area of the prosome and of the total body is of interest and concern because of the variable orientation which zooplankton may assume during processing. In the present study measurements for copepods were based on prosome lengths and surface areas. The reasons for choosing these measurements were two-fold: 1) prosome area was chosen because the positioning of individuals at the time of processing was highly variable and it was considered that prosome area would exhibit less overall variability than total body area and 2) the inclusion of antennae, appendages and the urosome could also have introduced additional variability into length measurements relative to prosome lengths. Previous studies of copepods have generally measured prosome lengths so a degree of comparability between measurements is maintained.

The experiment examining prosome and total body areas shows that, despite variability in individual measurements, there appears to be a predictable relationship between prosome surface area and total body surface area over a range of sizes. This suggests that measurements of total body area would have been acceptable to use, at least for the three taxa examined.

Problems associated with the orientation of zooplankton when using image analysis have been noted in previous studies (Jeffries *et al.* 1980, 1984; Dietrich and Uhlig 1984; Gorsky *et al.* 1989). Jeffries *et al.* (1980, 1984) also noted that the low contrast of planktonic animals made them difficult to process. A possible solution to the problem of orientation may be the use of live animals which tend to adopt more uniform positions (Dietrich and Uhlig 1984; Gorsky *et al.* 1989). *In situ* videos, silhouette photography (Jeffries *et. al.* 1984) and narcotising agents (Dietrich and Uhlig 1984) have also been suggested as potential solutions for combatting this problem.

The use of image analysis in processing marine plankton dates from

the mid 1970's, yet today it is still not routinely used in most plankton studies. There are probably several factors contributing to this lack of application including the expense of equipment and the specialised nature of its operation. Despite recent advances towards user-friendly systems (e.g. Estep *et al.* 1986) image analysis remains a fairly complicated business. Other considerations are the time required to get a system up and running for processing samples. Without prior experience, this can represent a considerable investment in time; if only a few measurements are required the temptation would surely be to make them by hand. Even once a programme has been developed there are constraints within the system itself. Magnification, discrimination levels and overlapping objects all represent potential sources of error particularly with respect to measurement data. In addition, size measurements are still only 2-dimensional and must be converted to biovolumes using appropriate geometrical approximations.

Despite its limitations, image analysis still offers great potential for the automated processing of marine plankton and the acquisition of biological data at resolutions comparable to that for physical processes. Measurement data obtained using image analysis techniques may never be as 'accurate' as traditional methods, but these too are subject to variability depending upon the magnification used (see Gorsky *et al.* 1989). It is already accepted that one often cannot count all planktonic organisms in a sample, and even counting the entire sample may provide only an approximation of the real distributions and abundances in the wild (e.g. the sampling window referred to by Angel (1977)). Sub-sampling prior to enumerating plankton samples is now an accepted practice. In a similar manner, the greater volume of data which may be acquired using image analysis techniques may outweigh any measuring errors and the loss of taxonomic and/or developmental information.

The ultimate goal of image analysis, the incorporation of pattern

recognition, remains a long way in the future. This will require the acquisition of large volumes of statistical data regarding the morphometrics of planktonic taxa in order to provide the library of information required to distinguish between different species. Initial work (e.g. Jeffries *et al.* 1980, 1984) has shown that it is possible to acquire this information on a coarse scale, which will enable broad taxonomic groups to be studied. However, the importance of information at the species level in order to fully understand how ecosystems function is now recognised (e.g Davis 1984) and eventually more detailed information will be required.

For the size measurements the ultimate goal will be to relate the areal measurements to equivalent carbon units. Båmstedt (1981) examined the relationship between water and organic content for a number of boreal macrozooplankton taxa. It may be possible to expand this work to include the relationship between projected surface area, water content and organic content. Such a relationship would need to be examined for different taxa and developmental stages, as well as seasonal and geographical affects.

Image analysis was successfully used in the present study to obtain measurement data for individual zooplankters. However, a considerable investment of time was required to develop the programme which, once up and running, still required the continual presence of an operator. Although image analysis does offer great potential for the routine processing of zooplankton samples, much work is still required in order to develop a fully automated programme for general use by planktologists. In its present state, it is questionable whether the extra measurement data obtained using this technique warrants its application in routine zooplankton work.

In summary, the greater volume of data obtainable by using image analysis may outweigh any errors associated with the technique. However, it would appear that much thought needs to be given to the use of image

analysis in plankton studies. There is always a danger of developing the science to fit the technique, not the reverse which is clearly desirable. It may be that for some studies, such as those requiring detailed taxonomic and/or developmental information, image analysis will not be suitable.

5.2 ZOOPLANKTON ASSEMBLAGES

5.2.1 Total Zooplankton Numbers and Biomass

Marked differences in total zooplankton numbers and biomass and their partitioning within different size fractions were observed between the four regions examined and between the two cruises.

In March, comparable results were obtained for total zooplankton numbers and biomass at both 10 and 30m. Numbers were generally low throughout the study area but relatively higher in the Firths of Lorn and Clyde than in the North Channel and on the Malin Shelf. Small animals predominated especially in the North Channel and on the Malin Shelf. In contrast, larger individuals were more abundant at stations near Arran in the Firth of Clyde. Biomass in March was uniformly low at <1 ml m^{-3}.

In May, zooplankton numbers and standing stocks were higher than those observed in March in most areas. The greatest increases were observed in Loch Fyne and in Kilbrannan Sound in the samples at 10m. Small zooplankton predominated on the Malin Shelf and in the Firth of Lorn, although larger animals were more abundant in the latter region than was observed in March. Larger individuals also predominated in Loch Fyne and at stations near Arran, including Kilbrannan Sound. Conditions elsewhere in the Firth of Clyde were variable.

The low zooplankton numbers and standing stocks observed in March and the subsequent increase in May is typical of zooplankton assemblages

in temperate/boreal waters for pre- and post bloom periods (e.g. Williams and Lindley 1980). Zooplankton standing stocks are generally at a minimum at the time of the spring phytoplankton bloom (e.g. Eriksson 1973; Colebrook 1979; Båmstedt 1981), and depending on their size may attain maximum numbers between one and three months later (e.g. Cushing 1975; Krause and Trahms 1983). Since the timing of the spring phytoplankton bloom exhibits considerable variability due to factors related to latitude and local hydrographic conditions, (e.g. Syvitski *et al.* 1987; Båmstedt 1985) the timing of maximum zooplankton standing stocks may also exhibit considerable local variability. For example, in Balsfjorden (69°N), located in northern Norway, zooplankton standing stocks reach a maximum in September (Hopkins 1981), while in the Hardangerfjord (60°N) the maximum occurs in July (Lie 1967). Båmstedt (1988) also maintained that the magnitude of the zooplankton standing stock is influenced by water-column depth (see also Matthews and Heimdal 1980).

Information regarding the specific timing and magnitude of the spring bloom throughout the study area is sparse. Boney (1986) reported that the spring bloom in the Firth of Clyde typically occurs in late March. Similarly, Tett *et al.* (1986) noted that the spring bloom in Loch Striven occurs in late March or early April. In the Firth of Lorn, where freshwater outflow and mixing may be considerable, the bloom may be delayed until April or May. On the Malin Shelf, the timing of the spring phytoplankton bloom will be influenced by the development of thermal stratification in the near-surface layer and is likely to occur in April/May as opposed to March as reported for the Firth of Clyde. This would suggest that zooplankton standing stocks measured during May 1986 represent close to the maximum values obtained for assemblages in the Firth of Clyde, but possibly not for those in the Firth of Lorn and on the Malin Shelf. Observations from the Firth of Clyde are consistent with this idea. Adams (1986) reported that zooplankton standing stock

in the Firth of Clyde, based on collections from a 250μm net, began to increase rapidly in March and reached peak values in April.

It is difficult to compare estimates of zooplankton standing stocks between studies, due to the many potential sources of variability deriving from differences in the collection and processing of samples. Nonetheless, bearing this in mind, it is useful to compare data collected during this study with those available from other fjord and continental shelf systems (Table 5.2).

The estimates of standing stock shown in Table 5.2 generally represent the maximum levels attained by zooplankton assemblages in each of the respective areas. When these values are compared with those from throughout the study area in May, the time of maximum biomass (Figures 4.14 and 4.16 and Appendix 9), it is clear that standing stocks in many areas, particularly stations around Arran in the Firth of Clyde, the outer Firth of Lorn, and the North Channel are considerably higher than those recorded from other fjord and continental shelf systems.

There are several factors which may have contributed to the relatively high levels of standing stock recorded in the present study. The different method of sample collection (i.e pump instead of net) is likely to have had a marked effect on the recorded levels of standing stocks. Net samples integrate zooplankton biomass over large areas of the water column and therefore can result in relatively lower estimates of standing stock due to patchy distributions. In contrast, discrete-depth samples collected by pump are more likely to produce high values of standing stocks if a patch is encountered. In Loch Fyne, the anomalous nature of the value obtained at 10m, combined with the low volume of water filtered, suggests that a patch was encountered during sampling and may have partially clogged the filter. The zooplankton biomass measured at this station may therefore not be representative of the area in general. In addition, several of the studies used mesh sizes greater than 333μm which was the upper limit for the fine size fraction

Table 5.2 Estimates of zooplankton standing stocks obtained from the literature for selected fjord and continental shelf regions. All biomass values (Bio) have been converted to wet weights expressed as ml m^{-3} for comparison with results in the present study. - indicates information was not available.

Location	Reference	Equipment	Mesh	Year	Month	Depth	Bio
FJORD SYSTEMS							
NORWAY							
Hardangerfjord	Gundersen 1953	Nansen net (0.72m dia)	No 8	1950	July	0-50m	0.45
"	Lie 1967	"	200µm	1956	July	0-100m	0.12
" (entrance)	"	"	"	1956	April	0-100m	0.16
Skjomnen, Inner	Strømgren 1974	Juday net (0.1m2)	190µm	1970	June	0-35m	1.14
" , Outer	"	"	"	1970	June	0-150m	1.00
Korsfjord	Matthews and Bakke 1977	Longhurst frame net (.33m dia)	500µm	1971	August	0-650	0.12
Balsfjorden	Hopkins 1981	Bongo net (.25m dia)	500µm	1976	September	0-190m	0.75
SWEDEN							
Kosterfjorden	Båmstedt 1988	conical net (1m dia)	400µm	1976	October	0-200m	0.32
Kungsbacka Fjord	Olsson and Ölundh 1974	Nansen net (.5m dia)	160µm	1969	June	0-16m	0.79
SCOTLAND							
Loch Striven	Wren 1991	modified WP-2 Net	200µm	1990	June	0-30m	8.00
Loch Etive	Mauchline 1987	conical net (.45m dia)	660µm	1978	September	0-120	0.10
			237µm	"	"	"	0.12
			108µm	"	"	"	0.03
Firth of Lorn	present study*	submersible pump	330µm	1986	May	10m	0.18
Firth of Clyde	present study*	submersible pump	330µm	1986	May	30m	50.62
CANADA							
Saguenay fjord	De Ladurantaye *et al.* 1984	Bongo net (0.25m dia)	158µm	1975	May	-	1.50
CONTINENTAL SHELF SYSTEMS							
Flemish Cap	Anderson 1990	Bongo nets (.61m dia)	333µm	1981	May	-	0.65
		"	165µm	"	"	-	0.75
		ring net (.5m dia)	80µm	"	"	-	2.10
Scotian Shelf	Mills and Fournier 1979	conical net (0.37m dia)	239µm	-	-	0-90m	0.10
Georges Bank	Sherman *et al.* 1987	Bongo nets	333µm	**	May/June	-	1.04
North Sea	Krause and Martens 1990	WP-2 net	200µm	1986	May/June	0-20m	>2.00
Malin Shelf	present study*	submersible pump	330µm	1986	May	10	2.75

* see also Appendices 9 and 10
** five year mean

used in the present study. This fraction was an important component of the biomass at stations in the Firth of Lorn, North Channel and on the Malin Shelf during the May cruise. Data collected by Anderson (1990; Table 5.2) also illustrate the effect that mesh size can have on estimates of standing stocks. Although data were collected for three size fractions in the present study the results suggest that the pump was ineffective in collecting animals >1000μm in size (i.e. the coarse size fraction).

In the Firth of Clyde, high standing stocks were generally observed in the deep water mass around Arran and Loch Fyne (even taking into account any clogging). Stations in these areas were in deep water (>100m) and the biomass largely consisted of the medium fraction. These samples contained large numbers of *Calanus* spp. which may have undertaken diel vertical migrations into the near-surface layer from the deeper water below. *Calanus* adults and stage V copepodids are also known to overwinter in deep waters, migrating into the surface layer to reproduce during the spring (e.g. Williams and Conway 1988; Sameoto and Herman 1990). In the northern North Atlantic the spring migration of *C. finmarchicus* occurs in April/May (Williams and Conway 1988). It is probable that the deep waters surrounding Arran and in Loch Fyne provide an overwintering refuge for *C. finmarchicus*, and the increased standing stocks observed in May could be partly due to the spring migration of these individuals into the surface layers to spawn. This is consistent with the comment of Adams (1986), in his review of zooplankton assemblages in the Firth of Clyde, that *Calanus* spp. occurred in enormous numbers in the surface layers during May and June, and in large numbers during autumn and winter below depths of 100m, particularly in Loch Fyne.

Physical processes may have been responsible for the high standing stocks observed at station Z4 in the North Channel where one would not generally expect high values due to the turbulent nature of the area

resulting from tidal currents (e.g. Edwards et al. 1986). The high biomass observed at this station may represent an advection of material from the Irish Sea to the south. Barnes (1950) concluded, based on the occurrence of *Sagitta setosa*, that Irish Sea water was transported into the Firth of Clyde during the autumn. The presence of the 34°/∞ isohaline in May suggests a direct flow of water from the Irish Sea through the North Channel.

The high standing stocks observed at station FL8 in the outer Firth of Lorn and station M3 on the Malin Shelf may be related to the presence of the Islay Front which was situated in this region during the May cruise. Frontal regions are known to be areas of increased biological material (e.g. Pingree *et al.* 1978; Simpson *et al.* 1979; Floodgate *et al.* 1981; Simpson *et al.* 1982; Hesse *et al.* 1989) although whether this represents increased productivity is of considerable debate (see Le Fèvre 1986). Floodgate *et al.* (1981) found that zooplankton numbers were between two and eight times higher than those observed on either side of a front located in Liverpool Bay. Kahru *et al.* (1984) found zooplankton biomass to be twice as great on the high-salinity side of a frontal region in the Baltic Sea than in the low-salinity region. Scrope-Howe and Jones (1985) found increased numbers of nauplii of *Acartia clausi* and *Pseudocalanus elongatus* in the Irish Sea frontal zone which they attributed to increased production and not physical aggregation. In the present study, the high zooplankton biomass observed at stations in the region of the Islay Front, relative to those in the Firth of Lorn and at the edge of the Malin Shelf, suggest that the increased values were related to the frontal system. Whether or not this increased biomass represents advective accumulation or *in-situ* growth could not be determined from the available data.

Regardless of the controlling mechanisms, and taking into account the different sampling regimes, there can be no doubt that some regions of the study area contain high zooplankton standing stocks, particularly

stations in the Firth of Clyde. That this is not totally an artifact of the sampling method used in the present study is confirmed by the relatively high values obtained for Loch Striven by Wren (1991).

The results regarding the partitioning of biomass between cruises provide some insight into the faunal groups which were, on a coarse scale, important in the pre- and post-spring bloom conditions. (These results do not take into account regional differences which are discussed in section 5.2.3). Overall, the fauna in March was characterised by large numbers of meroplankton, particularly cirripede nauplii, and also copepod nauplii. Meroplankton are often common components in pelagic zooplankton collections (e.g. Eriksson 1973; Olsson and Ölundh 1974; Falk-Petersen 1982; Krause and Trahms 1982; Lindley 1988; Bosselmann 1989) and at times may numerically dominate the fauna (e.g. Olsson and Ölundh 1974). Studies have shown that the release of pelagic larvae by benthic organisms is synchronous with the spring bloom (Falk-Petersen 1982; Krause and Trahms 1982) including the release of nauplii by barnacles (e.g. Barnes 1962; Starr *et al.* 1991).

Meroplankton also accounted for considerable proportions of the overall biomass during the March cruise. This is similar to results obtained by Olsson and Ölundh (1974) who found that up to 90% of the zooplankton biomass in Kungsbacka fjord on the west coast of Sweden could be attributed to meroplankton during the spring and autumn. Copepod eggs and nauplii can also attain high abundances (Falk-Petersen 1982) and may represent an important source of zooplankton biomass and production (e.g. Petersen *et al.* 1991). In the Skagerak, Peterson *et al.* (1991) found that copepod nauplii accounted for between 5 and 21% of mean copepod biomass and 16% of total production.

The higher zooplankton abundances and standing stocks observed in May resulted from large numbers of copepods, particularly *Calanus* spp.; increased numbers were also observed for other species such as *Pseudocalanus* spp., *Temora longicornis*, *Acartia clausi*, and *Centropages*

hamatus. This was accompanied by a decrease in the relative proportion of larval stages and meroplankton in the fauna. This shift to a copepod dominated fauna composed of only a few main species is common for fjord and shelf waters (e.g. Deevey 1956; Wiborg 1954; Lie 1967; Hopkins 1981; Anderson 1990). For example, Anderson (1990) found that copepods accounted for approximately 50% of the total zooplankton biomass (>333μm) on the Flemish Cap in late March, increasing to >90% by August, although meroplankton did not constitute an important source of biomass at the earlier date. The dominance, both in terms of numbers and biomass, of fjord and shelf zooplankton faunas by *Calanus* spp. is well documented (e.g Wiborg 1954; Marshall and Orr 1955; Lie 1967; Strømgren 1974; Matthews and Bakke 1977; Fransz and van Arkel 1980; Scrope-Howe and Jones 1985; Peterson *et al.* 1991).

5.2.2 Species Distributions and Relative Abundances

The distributions and relative abundances of zooplankton during the two cruises provided information regarding the importance of individual species and other taxa within the fauna of the different regions.

In March there were differences in the faunal composition among the various regions, but only slight differences between the two depths. *Calanus* spp., *Pseudocalanus* spp., *Acartia clausi*, *Oithona spp.*, and *Microcalanus* spp. were generally widespread throughout the study area, at both depths sampled, although abundances varied. *Temora longicornis* also occurred throughout the study area with the exception of the Malin Shelf, in keeping with the neritic distribution of this species (e.g. Colebrook *et al.* 1961; Colebrook 1964). All the above-mentioned species are widespread and most are common members of the zooplankton faunas in Norwegian (e.g. Lie 1967; Strømgren 1974; Hopkins 1981) and Swedish (e.g. Eriksson 1973; Olsson and Ölundh 1974) fjord and shelf waters

(e.g. Wiborg 1954; Skreslet and Rød 1986), Scottish lochs (Marshall 1949; Adams 1986; Mauchline 1987; Wren 1991), the North Sea (e.g. Gibbons 1936; Williams and Lindley 1980; Krause and Trahms 1982; Krause and Martens 1990), and coastal waters off eastern Canada (e.g Davis 1982; Tremblay and Roff 1983*a*; Brown and Gaskin 1988; Citarella 1989) and the United States (e.g. Davis 1987). Abundances vary locally depending on the hydrographic conditions, and other factors, such as depth, may also influence distribution patterns. This is illustrated by *Calanus* spp. where water-column depth is known to be an important factor in determining the locations of overwintering populations (e.g. Skreslet and Rød 1986; Sameoto and Herman 1990; Herman *et al.* 1991). The fact that *C. finmarchicus*, which in this study consisted of stage C5 and adults, was a common member of the zooplankton fauna at 30m but not at 10m is possibly related to the typically deeper distribution of the older life-history stages in the water column (Marshall and Orr 1955).

The relatively higher zooplankton numbers of copepodid nauplii, early copepodid stages, and euphausiid eggs and nauplii in the Firth of Clyde are consistent with the concept of the spring bloom beginning earlier there than in other areas examined in the study. The initiation of spawning by copepods following the spring bloom was estimated to be on the order of 3 days for copepods in the northern North Sea (Krause and Trahms 1983). Anderson (1990) recorded numbers of copepod nauplii averaging $180m^{-3}$ during the first week of April increasing to about $1200m^{-3}$ by the first week of May for copepod assemblages on the Flemish Cap. These numbers are comparable to those recorded in the present study during March in the outer Firth of Clyde at 10m ($\sim 1000m^{-3}$). The greater abundance of copepod nauplii at 10m than at 30m may have been related to higher phytoplankton biomass although no clear pattern is evident from the corresponding chlorophyll *a* data.

The fauna in the Firth of Lorn during March was characterised by high numbers of meroplankton, particularly cirripede nauplii. Low

numbers of most common copepods also occurred at various stations throughout the firth as did small numbers of unidentified copepodids and nauplii. Measurements of chlorophyll *a* made during the March cruise showed increased levels of phytoplankton biomass (6.71µg l^{-1} at station FL15; Jones 1988*a*) possibly suggesting an 'early' spring bloom was under way. Much phytoplankton production in early spring blooms is thought to sediment to the seabed (Båmstedt 1985; Keller and Riebesell 1989), although it may also trigger spawning in zooplankton (Båmstedt 1985) and benthic organisms (Starr *et al.* 1991). Melle and Skjoldal (1989), however, found evidence of reduced spawning success in *Calanus finmarchicus* associated with an early spring bloom in the Barents Sea. If the March standing stocks are taken to be representative of the magnitude of the overwintering zooplankton populations in the Firth of Lorn this could explain the low numbers of copepod nauplii, and the high numbers of meroplankton occurring at this time.

On the Malin Shelf, the fauna was composed primarily of small copepods, i.e. *Oithona* spp., *Pseudocalanus* spp., *Acartia clausi*, and *Paracalanus parvus*. The small numbers of copepod nauplii collected at 10m and unidentified copepodids collected at 30m are consistent with the theory that the spring bloom was not yet under way in the shelf waters.

In May, the composition of the fauna was largely the same, but with shifts in relative abundances of species. Increased numbers, compared with March, were observed for most copepods throughout the study area. In the Firth of Clyde, large numbers of *Calanus* spp. and *C. finmarchicus* were associated with the high standing stocks recorded near Arran and in Loch Fyne. Other common species, e.g. *Pseudocalanus* spp., *Microcalanus* spp., *Acartia clausi*, *Temora longicornis* and *Centropages hamatus* also showed increased numbers. Copepod nauplii and copepodids were abundant in the firth suggesting that spawning continued into May. This is consistent with earlier observations made by Marshall (1949) for the copepod fauna in Loch Striven.

In the Firth of Lorn meroplanktonic taxa occurred in the fauna in May, along with increased numbers of the copepods *Acartia clausi*, *Temora longicornis*, and *Centropages hamatus*. These three copepod species are known to be capable of producing dormant eggs (see Grice and Marcus (1981) for clarification of the terms 'resting' versus 'dormant') as a means of continued population survival following periods of unfavourable environmental conditions (e.g Uye 1985). Lindley and Hunt (1989) concluded that resting eggs were an important overwintering mechanism for two copepod species in the North Atlantic and North Sea.

Resting eggs may be either 'in diapause' or 'quiescent' and the nature of the dormancies is very different (Grice and Marcus 1981). Diapause refers to arrested growth which is a genetic adaptive response to unfavourable environmental conditions; this response is triggered by an external stimulus prior to the onset of the poor conditions. Quiescence is a state of retarded development caused directly by harsh environmental conditions and development resumes once conditions are favourable.

Dormant eggs have been collected from a wide range of water depths and regions and for a number of taxa (e.g. Uye *et al.* 1979; Marcus 1984, 1989, 1990; Marcus and Fuller 1989; Lindley 1990; Næss 1991). Lindley (1986) found dormant eggs of three copepod species, including *T. longicornis*, in bottom sediments collected from depths of between 19 and 50m in the English Channel and North Sea. Marcus (1990) found dormant eggs of copepods, including *A. clausi*, cladocerans and a rotifer up to 10cm deep in bottom sediments and at water depths of between 60 and 120m off northern California. She concluded that this could represent a considerable source of nauplii for the pelagic fauna with egg concentrations for *A. clausi* as high as 10^5 m^{-2} and a 40 to 50% hatching success rate. Næss (1991) observed high egg densities of up to 2 x 10^6 m^{-2} in an enclosed Norwegian basin during the autumn. Factors including light (Marcus 1990), temperature (Uye *et al.* 1979; Sullivan and McManus

1986) and oxygen (Uye *et al.* 1979) are all thought to affect hatching success. Recent work (Marcus and Schmidt-Gengenbach 1986) has also suggested that bioturbation by benthic animals may contribute to the hatching success of dormant eggs (Marcus 1990).

There are no direct observations in the present study to suggest that dormant eggs may be an important mechanism for the recruitment of copepod populations in the Firth of Lorn. However, Lindley (1990) predicted, on the basis of water depth, the difference between the water depth and the depth of the tidally mixed bottom layer ($H-\partial$), and bottom stress due to tidal currents, those areas in the seas surrounding the British Isles where copepod eggs were likely to be abundant in bottom sediments. The areas identified using these criteria included the Firth of Lorn out to the Islay Front and the outer region of the Firth of Clyde near the Davaar Sill (Lindley 1990). Given the low March standing stocks, the increased numbers of *T. longicornis*, *A. clausi*, and *C. hamatus* observed in the Firth of Lorn during May suggest that dormant eggs may be an important mechanism of species recruitment in this region.

Two cladocerans, *Evadne nordmanni* and *Podon leuckartii*, also occurred in relatively large numbers in the Firth of Lorn in May. The reproductive strategy of these animals includes sexual reproduction to produce resting eggs and reproduction by parthenogenesis during favourable environmental conditions (Onbé 1985). Such a reproductive strategy allows the establishment of large populations over very short time periods (Poggensee and Lenz 1981). These neritic cladoceran species are often common members of the zooplankton fauna in boreal/temperate waters from spring to late autumn (Gieskes 1971). Resting eggs are thought to be the primary overwintering mechanism and means of species recruitment in the spring (Gieskes 1971; Onbé 1985). This strategy for avoiding harsh environmental conditions during the winter would account for the sudden appearance of *E. nordmanni* and *P. leuckartii* in the Firth

of Lorn during May.

On the Malin Shelf, large numbers of copepod nauplii were observed in May relative to March. This is consistent with the idea that the spring bloom occurred later on the shelf than in the inshore waters, particularly the Firth of Clyde. Copepodids of *Calanus* spp. occurred at the outermost station on the Malin Shelf although adults of neither *C. finmarchicus* nor *C. helgolandicus* were collected. Adult stages of these two species were, however, collected at station M3 in the frontal region which may represent a source of advected material for the outer shelf region.

5.2.2.1 Indicator Species

Due to their widespread abundance, none of the common species collected in the present study was of use as an indicator species (e.g Russell 1935; Fraser 1952) in demonstrating faunal assemblages associated with any particular region of the study area. However, several species were associated only with the warm, saline water mass offshore: *Clausocalanus* spp., *Ctenocalanus vanus*, *Euchaeta acuta* Giesbrecht, *Calocalanus styliremis*, and *Neocalanus tenuicornis* (Dana) all occurred in low numbers, and only at stations on the Malin Shelf. Their association with this particular region of the study area is ascribed to their typically oceanic origins (e.g. Rose 1933; Colebrook *et al.* 1961; Frost and Fleminger 1968).

5.2.3 Multivariate Analyses

The multivariate analyses showed that station groups could be identified throughout the study area. Although there was variability between depths within cruises, and between cruises, groups often showed an affinity to a particular geographical region. This was most

pronounced for stations located on the Malin Shelf and in the Firth of Lorn. Station relationships within the Firth of Clyde and North Channel were more complex.

Stations on the Malin Shelf generally remained distinct from those in other regions of the study area. The segregation of stations on the Malin Shelf from those in the outer Firth of Lorn corresponded with the position of the Islay Front and suggests that the front represented a faunal boundary between the two regions. However, on two occasions at 30m, station groups transgressed the frontal region and a station in the outer Firth of Lorn clustered with those on the Malin Shelf. The fact that this occurred at 30m, and not at 10m, may have indicated that the front was primarily a surface feature. However, evidence to the contrary was presented by May (1987; figure 4) in contoured plots of temperature, salinity and σ_t for the Malin Shelf at the time of the May cruise. In all plots, the Islay Front was clearly shown to extend throughout the water column. No comparable plots are available for the March cruise.

Stations in the Firth of Lorn were also generally distinct from those in other regions of the study area. Groups were typically associated with 'inner' and 'outer' regions of the firth, although station FL15 exhibited greater variability in its relationship with other stations. In March, at 10m, station FL15 was distinct from other stations in the Firth of Lorn, while in May the station was loosely clustered with stations in the Firth of Clyde and North Channel. Station FL15 is located at the outflow of Loch Etive, a contiguous sea-loch of the Firth of Lorn, and is therefore influenced by the tidal exchange of water across the loch sill. The variable position of this station within the multivariate clusters was probably related to the dynamic local hydrographic conditions.

Relationships among stations in the Firth of Clyde and North Channel were variable both within and between cruises. In March, at 10m, stations comprising the multivariate groups and subgroups were located

throughout the region without a well defined geographical pattern. At 30m, more organisation was evident although in both cases stations in the outer Firth of Clyde were separate from those in the North Channel. This may have been related to the presence of the Great Plateau Front located at the entrance to the firth. In general, conditions throughout the area in March were probably variable with respect to parameters such as surface heating, freshwater outflow and chlorophyll *a* biomass. The patchy distribution of station groups observed at this time probably reflected the response of zooplankters to local conditions.

In May, clustering was tighter among stations in the outer Firth of Clyde and North Channel than in March, and this was more pronounced at 30m than at 10m. Stations around Arran and in Loch Fyne were distinct from those in the outer Firth of Clyde and North Channel. The separate clustering of the Loch Fyne station at 10m may have been the result of a clogged filter, as previously discussed (p. 263). The Arran Deep group was related to large numbers of *Calanus* spp. which dominated the fauna in this region. Stations in the outer Firth of Clyde and North Channel formed a single group in May at both depths. This contrasted with the situation in March, despite the presence of the Great Plateau Front on both occasions.

Examples from the literature where frontal regions represent distribution barriers can be found for phytoplankton (Hara and Tanoue 1985; Hesse *et al.* 1989), zooplankton (Iverson *et al.* 1979; Smith and Vidal 1984) and larval fish (Iwatsuki *et al.* 1989). Andreu *et al.* (1989), however, found that a frontal region in the Indian Ocean did not constitute a barrier to the distribution of chaetognaths, while Kahru *et al.* (1984) found the composition of zooplankton on either side of a salinity front in the Baltic Sea to be similar. Further work is needed in the region of the Islay and Great Plateau Fronts to determine how these systems may affect the dispersion of zooplankton between the coastal and shelf waters.

Of the several parameters examined in relation to the station groups, salinity, followed by temperature, showed the strongest overall associations with the observed patterns. Chlorophyll *a* and depth occasionally appeared related to individual groups or subgroups, but no clear pattern emerged. The association of temperature and salinity with the observed station clusters is not unexpected. Temperature and salinity, which characterise different water masses, represent regions where differing combinations of physical and biological parameters interact to produce characteristic faunal assemblages (e.g. Gardner 1977; 1980). In the present study the distribution of temperature and salinity reflected an inshore/offshore gradient progressing from cold, fresh waters inshore to warm, saline waters offshore. Tremblay and Roff (1983*a*) also found faunal assemblages that reflected inshore/offshore temperature and salinity gradients in the Scotian Shelf region.

The relationship between zooplankton assemblages and chlorophyll *a* measurements is not as straightforward as in the case of salinity and temperature. Some studies have noted a positive correlation between chlorophyll *a* and zooplankton biomass (e.g. Kozasa 1977; Yoshioka *et al.* 1985; Scrope-Howe and Jones 1986) while others have not (e.g. Le Borgne *et al.* 1985; Gibbs *et al.* 1991). Roff *et al.* (1988) found a significant correlation between phytoplankton abundance (estimated according to the greenness of the samples) and copepod abundances for zooplankton off the Northumberland coast when a two-month lag between peak values was taken into account. Other studies have found that copepods are associated with areas of maximum primary production rather than biomass (e.g. Longhurst 1976*b*; Herman *et al.* 1981; Herman 1983; Fiedler 1983).

The fact that no clear relationship was observed between station clusters and chlorophyll *a* does not indicate that this parameter was unimportant in the organisation of station groups in the present study. There are several factors which may have contributed to the lack of correlation between the two variables. Zooplankton were collected at

discrete depths while the estimates of chlorophyll *a* biomass represented integrated values for the euphotic zone. Zooplankton are known to aggregate in the region of the chlorophyll maximum when grazing (e.g Haury 1976; Bird 1983; Paffenhöfer *et al.* 1984; Townsend *et al.* 1984; Sameoto 1984; Scrope-Howe and Jones 1986), with larger individuals undertaking diel vertical migrations to feed in the surface layers at night (e.g Baars and Oosterhuis 1984; Tselius 1988; Rosenberg *et al.* 1990). The zooplankton samples in the present study were collected at 10m and 30m and the depth of the chlorophyll maximum relative to the sampling depths is likely to have varied between stations. These differences may have obscured any relationship between zooplankton distributions and phytoplankton biomass. In addition, depending on the magnitude and size composition of the overwintering zooplankton assemblage, the response time of the fauna to increases in phytoplankton biomass will vary. This would also make it difficult to discern any overall pattern on a large spatial scale such as that in the present study.

Depth was not strongly related to station groups in the present study although occasionally stations within subgroups were all of similar depths. Sabatès *et al.* (1989) found the distribution of zooplankton in the western Mediterranean to be strongly correlated with station depth with most groups having greater abundances in the deeper shelf/slope region. Increased zooplankton biomass associated with deeper water in fjords has already been discussed (see section 5.2.1). The faunal assemblages of surface waters overlying deeper regions could differ from those in adjacent, shallower areas through the diurnal migrations of animals inhabiting the deeper water mass. This was, however, not observed to any great extent in the present study.

Physical factors which were not specifically examined in the present study, but which may have contributed to the observed station groups, were water column stability and station distance from shore.

Both factors have been found to influence zooplankton community structure on the Scotian Shelf (Tremblay and Roff 1983*a*) and in the Mediterranean (Sabatès *et al.* 1989).

5.2.3.1 Faunal Assemblages

Faunal assemblages could be characterised for each of the station groups identified using multivariate analyses on the basis of the corresponding data for rank order abundances of species. Although the clustering of stations was variable both within and between cruises, station groups did show a general association with particular regions of the study area, and these corresponded with different faunal assemblages.

The faunal assemblage on the Malin Shelf was characterised by small copepods. Meroplankton, primarily as cirripede nauplii, occurred seasonally in the plankton as was observed in March. In May, small copepods still predominated although *Calanus* copepodids were most abundant at 10m.

In the Firth of Lorn the faunal assemblage in March consisted primarily of meroplanktonic taxa. These figured prominently in May, although small copepods and cladocerans also occurred at this time.

The North Channel/Outer Firth of Clyde region, though less well defined spatially than the other regions of the study area, was generally characterised by a mixture of small copepods, with meroplankton also prominent in March. This contrasted with the assemblage in the Arran Deep and Loch Fyne which was *Calanus*-dominated during both sampling periods.

The factors contributing to these different faunal assemblages are likely to include water depth and stability, and the timing and magnitude of the spring bloom. These factors all exhibited considerable variability throughout the study region.

As previously discussed, the deep waters surrounding Arran and in Loch Fyne provide an overwintering refuge for *Calanus* populations in the Firth of Clyde. However, differences in primary production measured in the Firth of Clyde, relative to the Firth of Lorn and on the Malin Shelf, may also have contributed to the *Calanus* dominated fauna in this region. The results of studies examining the relationship between reproductive response and food concentration suggest that small copepods such as *Acartia clausi*, *Paracalanus parvus*, *Pseudocalanus* spp. and *Oithona* spp. are able to initiate spawning and maintain maximum rates of egg production at lower phytoplankton concentrations than required by *Calanus* (Runge 1988). The presence of large *Calanus* populations in the Arran Deep and Loch Fyne may therefore also be related to the typically higher levels of primary production in the Firth of Clyde, relative to the other regions of the study area. It is interesting however that estimates of primary production at some stations on the Malin Shelf were higher than those in the Firth of Clyde in March, but this may not have been representative. Alternatively, the lower production measured in the Firth of Clyde may have been the result of a higher grazing pressure exerted by the overwintering *Calanus* population. It is likely that depths on the Malin Shelf are insufficient for the region to harbour a large overwintering population.

Estimates of primary production in May were considerably higher in the Firth of Clyde than in the Firth of Lorn or on the Malin Shelf (see section 2.3.2). This may indicate that high levels of primary production are sustained for longer periods in the Firth of Clyde which could be important in maintaining the large *Calanus* stock.

In the Firth of Lorn, the faunal assemblage was very seasonal. Mixing throughout the water column, combined with a strong outflow in the near-surface layer, appears to prevent the establishment of a large, resident, holoplanktonic fauna. Resuspension of bottom sediments during mixing events, possibly associated with inflows of Atlantic water during

the winter months, may facilitate the hatching of dormant eggs thereby providing a mechanism for the establishment of copepod and cladoceran populations. However, the predominance of meroplankton in the fauna during both cruises suggests that the Firth functions primarily as a dispersal mechanism for benthic larvae.

The biomass and abundance spectra provided further information regarding the possible flow of energy within each area. The distribution of biomass within an ecosystem is often very different from the corresponding species abundance data. High abundances of an individual may or may not correspond with high biomass depending on its size. This was clearly illustrated in the present study by station groups on the Malin Shelf where the abundance and biomass spectra showed opposing patterns.

Although the biomass spectra examined in this study cover only part of a continuous spectrum they do illustrate that there were marked differences among the spectra between areas, and between cruises. This suggests that energy may be channelled through different pathways and that the fate of the material may also vary. When most of the biomass is comprised by larger animals, material may be more available to consumers at higher trophic levels and cycled through the food web more slowly. In addition, there is also a greater potential for material to be advected over long distances as larger animals generally have longer life spans (see below). In contrast, when most of the biomass is comprised by small individuals, material may be cycled through the food web more rapidly due to the typically shorter generation times. Correspondingly there is less potential for material to be exported or exchanged through larger-scale mixing processes.

Biomass in the *Calanus*-dominated assemblages in Arran Deep and Loch Fyne, biomass was high relative to other areas. However, most of the biomass was composed of *Calanus* copepodids and/or adults, and the copepodids were also numerically dominant. This contrasted with the

situation in the Firth of Lorn and on the Malin Shelf. In the Firth of Lorn, biomass was low and consisted mostly of meroplankton such as cirripede nauplii and decapod zoeae. Despite increased numbers of copepods in the May samples, none of the species contributed much to the biomass spectra. On the Malin Shelf, the abundance of small copepods represented a low biomass in the corresponding size classes of the biomass spectra although in all cases, biomass was concentrated in the larger size classes. In March this was due to small numbers of larger species (e.g. *Sagitta elegans* and *Parathemisto abyssorum*) and in May this was due to the presence of *Calanus* copepodids and adults.

Although biomass is not synonymous with production, smaller-sized individuals generally have shorter generation times than larger organisms, and the smaller the organism the higher the ratio of productivity to biomass (P/B; Banse and Mosher 1980; Grahame 1987; see also Table 5.3). Different sized assemblages can also reflect different food webs and this is further discussed in section 5.2.5.

In the Arran Deep and Loch Fyne where most of the biomass was composed of *Calanus*, turnover rates would be lower than in other regions, such as on the Malin Shelf, where the lower biomass consisted mostly of small copepods. In the Firth of Lorn, where most of the biomass was composed of meroplankton, it seems likely that energy in this system (i.e. primary and secondary production) is either advected offshore or channelled to the benthos. Lindley (1988) showed that the flux of material from the pelagos to the benthos was approximately three times greater than that from the benthos to the pelagos in a study of brachyuran production in the Irish Sea. In the Firth of Lorn, this is probably a combination of the low overwintering copepod standing stocks and the highly variable spring bloom.

5.2.4 Secondary Production and the Potential for Exchange

The exchange of planktonic material between regions within the study area depends on two factors: the prevailing current regime and local levels of production (Burrell 1988). Measurements of secondary production were not made in the present study although estimates of standing stock are available. These can be used to estimate production using P/B ratios. Such ratios have therefore been calculated for the copepod fauna at representative stations following the methods of Tremblay and Roff (1983*b*). Adult, female biovolumes were converted to organic weight by assuming the dry weight to be 20% of the wet weight, and organic weight to be 90% of the dry weight (Båmstedt 1981). Energy content for all species was estimated to be 25.24 kJ g dry wt^{-1}, using the equation of Båmstedt (1981; Table IV). Although this value will vary among species, the value used is in the middle of the range quoted by Tremblay and Roff (1983*b*) who reported an energy content of between 21-29kJ g dry wt^{-1} for copepods from the Scotian shelf. P/B ratios were calculated for each species using the Banse/Mosher equation:

$$\log P/B = -0.16 - 0.34 \ (\log M)$$

where M is adult body mass in kilocalories (1 kcal = 4.1855kJ; Tremblay and Roff 1983*b*).

Population biomass was determined for each species at each station using the individual measurement data from the image analyser. Total biomass for each species, as $mm^{-3}m^{-3}$, was converted to dry weight, assuming a 20% conversion, and multiplied by the energy content to convert to kJ m^{-3}. Although biomass values are only available for March and May, these have been converted to 'annual' values by multiplying their mean by 12. A coarse estimate of the 'annual'secondary production in each region of the study area was then obtained by multiplying the

P/B ratio by the mean 'annual' biomass. Production estimates at each station were made for the 10m and 30m samples separately and the mean values are presented in Table 5.3. It should be noted that although the production estimates are for the copepod fauna, they do not take account of naupliar production which can be considerable (e.g. Peterson *et al.* 1991). In addition, unidentified copepodids were not included in the estimates, though they were important components of the biomass at times, particularly in the Firth of Lorn during May.

Estimates of the annual rates of production for each region of the study area are shown in Table 5.3. These calculated values are comparable to those presented by Matthews and Heimdal (1980; table VI) for estimates of secondary production in several Scandinavian fjords and for fjord and shelf waters off the west coast of Canada.

Despite the coarseness of the estimates, these values do provide an indication of relative levels of production throughout the study area and are in agreement with the corresponding biomass data. The deep water surrounding Arran is highly productive relative to other regions of the study area, particularly the Firth of Lorn. Productivity on the Malin Shelf, though low, is still relatively higher than that in the Firth of Lorn. The high level of production calculated for the North Channel is interesting given the strong tidal currents which predominate in this area (Edwards *et al.* 1986). This value may not represent *in situ* production but rather an advection of material from the Irish Sea (e.g. Williamson 1956). However, Edwards *et al.* (1986) stated that stratification of the water column may develop in the deeper waters of the North Channel, such as at station Z4. Therefore it is possible that the relatively high production at this station is, at least partially, locally produced.

The results of this study clearly indicate that the Firth of Clyde may export a considerable amount of zooplankton into the contiguous shelf waters. Standing stocks and production levels are considerably

Table 5.3. Estimates of production/biomass (P/B) ratios and near-surface secondary production (copepods only) for stations representative of the four regions of the study area. Estimates of annual biomass and production have been derived using data only from March and May cruises, adjusted to obtain a mean 'annual' value. Details of the calculations, and their limitations, are given on p. 282.

FIRTH OF CLYDE

Station AB44	x 'Annual' Biomass (kJ m^{-3})	P/B	x 'Annual' Production (kJ m^{-3})
Calanus finmarchicus	199.67	6.71	1355.03
Pseudocalanus spp.	0.97	14.08	13.60
Acartia clausi	0.49	18.25	8.77
Microcalanus spp.	0.19	26.99	5.12
Temora longicornis	0.40	11.84	4.68
Centropages hamatus	0.19	11.81	2.21
Oithona spp.	0.06	30.11	1.60
		TOTAL =	1391.01

NORTH CHANNEL

Station Z4	x 'Annual' Biomass (kJ m^{-3})	P/B	x 'Annual' Production (kJ m^{-3})
Pseudocalanus spp.	10.34	15.54	157.65
Calanus finmarchicus	19.93	6.71	133.35
Temora longicornis	10.12	11.84	118.95
Acartia clausi	2.87	18.28	52.50
Centropages hamatus	1.57	11.81	18.54
Oithona spp.	0.33	30.11	9.83
Paracalanus parvus	0.27	21.51	6.28
Microcalanus spp.	0.01	26.99	0.17
		TOTAL =	497.27

FIRTH OF LORN

Station FL15	x 'Annual' Biomass (kJ m^{-3})	P/B	x 'Annual' Production (kJ m^{-3})
Pseudocalanus spp.	0.47	14.09	6.68
Temora longicornis	0.34	11.84	4.05
Calanus spp.	0.39	6.67	2.59
Centropages hamatus	0.16	11.81	1.88
Oithona spp.	0.04	30.11	1.11
Acartia clausi	0.02	18.28	0.31
Paracalanus parvus	0.01	21.51	0.23
Metridia lucens	0.02	8.23	0.17
Metridia longa	0.01	13.47	0.08
Microcalanus spp.	<0.01	19.68	0.07
Acartia discaudata	<0.01	8.37	0.02
Centropages typicus	<0.01	9.25	0.02
		TOTAL =	17.21

MALIN SHELF

Station FL0 & FL1	x 'Annual' Biomass (kJ m^{-3})	P/B	x 'Annual' Production (kJ m^{-3})
Calanus spp.	3.61	6.69	45.51
Oithona spp.	0.84	30.11	25.89
Pseudocalanus spp.	1.79	14.09	25.13
Acartia clausi	0.54	18.28	9.96
Paracalanus parvus	0.32	21.51	6.87
Ctenocalanus vanus	0.22	15.87	3.49
Centropages typicus	0.34	9.40	3.14
Metridia lucens	0.33	7.75	2.58
Neocalanus tenuicornis	0.07	9.88	0.65
Clausocalanus spp.	0.01	21.42	0.13
Temora longicornis	0.01	11.84	0.08
Calocalanus styliremis	<0.01	27.79	0.03
		TOTAL =	123.46

higher in the Firth and there are indications that spawning is initiated earlier in this region than in neighbouring waters. Station clusters identified in the multivariate analyses showed that faunal assemblages in the North Channel and outer Firth of Clyde were similar in May, particularly at 30m. This coincided with an increased flow in the Scottish Coastal Current which extended onto the Great Plateau at the Firth entrance and suggests that entrainment of zooplankton occurred at this time.

The fate of this advected material is subject to debate. Given the currents at this time of year, is seems likely that most of this material is advected to the Firth of Lorn, or through the Tiree Passage. Assuming a current speed of 5km day^{-1} in the North Channel (Simpson and Hill 1986) and a reduced speed of 3km day^{-1} outwith the channel west of Islay (Ellett and Edwards 1983; Economides *et al.* 1985), it would take approximately 31 days for a particle to travel from station AB14 on the Great Plateau to station FL12 at the entrance to the Firth of Lorn.

Marshall and Orr (1955) state that in the Clyde Sea area the time required for *Calanus finmarchicus* to develop from an egg to adult is approximately 30 to 35 days with a generation time of 60-70 days. They reported that the generation of *C. finmarchicus* which is present in the Clyde Sea Area during April and May remain almost entirely at the surface where they spawn in May. Such behaviour, i.e. a lack of diel vertical migration, would make the population more susceptible to entrainment in the Scottish Coastal Current.

Calanus was not a common member of the fauna in the Firth of Lorn during March but copepodids were more abundant in May. It is possible that the source of these copepodids was material entrained from the Firth of Clyde by the Scottish Coastal Current. However, the possibility of other sources, e.g. Loch Etive (see Mauchline 1987) or even deep pockets of water within the Firth itself, cannot be ruled out without more detailed investigation.

Production on the Malin Shelf is high relative to the Firth of Lorn and it is conceivable that the shelf region constitutes a source of zooplankton for the Firth under certain conditions. Mixing between the Atlantic and coastal water mass is restricted during the spring-autumn period by the presence of the Islay Front (Ellett 1979). It would appear that the frontal region also constitutes a faunal boundary between the inshore and offshore regions. However, during the winter months there is an onshore flow of deep, Atlantic water which penetrates into the Firth of Lorn. This may be an important 'seeding' mechanism which augments the low overwintering zooplankton standing stocks in this region. The fate of the advected material is likely to depend on the timing of the deep-water inflows relative to mixing events within the Firth and the development of the spring bloom.

The inshore waters also appear to be a source of plankton for the Malin Shelf during the winter/spring period as evidenced by the large numbers of meroplankton on the shelf, particularly during March. The occurrence of these species on the Malin Shelf again raises the question of the role of the Islay Front in the dispersion of inshore zooplankton. Skreslet and Rød (1986) interpreted the occurrence of *Munida sarsi* larvae, a common decapod found in Norwegian fjords, in waters 130 n. miles off of the Lofoten Islands as evidence that the fauna was derived from coastal waters. Due to the coarse level of identification for most meroplanktonic species in the present study, it is difficult to pinpoint their origin, other than being of 'inshore' as opposed to 'offshore' origin. However, their occurrence at the shelf edge does suggest that at least part of the fauna in that area is derived from inshore waters. The exact mechanism whereby this fauna arrives on the Malin Shelf is unknown. However, it is likely to constitute an important means of dispersal for meroplanktonic taxa in the study area.

Matthews (1986*b*) introduced the term "Ecology of Advection" and questioned the benefits of a life-history strategy which included the

loss of large proportions of the population through advective processes with no apparent potential for return back to the parent population. This appears to be the case with *Calanus finmarchicus* transported by the Norwegian Coastal Current (e.g. Skreslet 1983, 1986*b*) although there are examples where, through seasonal ontogenetic migrations, populations are able to exploit preferential habitats and recruit back into the original stock (Peterson 1979; Peterson *et al.* 1979).

In the present study, the *potential* for exchange among the various regions of the study area clearly exists. The Firth of Clyde is a prime candidate for exporting material to the contiguous regions, through entrainment by the Scottish Coastal Current. If this does occur, it would seem to constitute a situation similar to that in the Norwegian Coastal Current, i.e. the transport would be unidirectional. It is difficult to imagine how, with the prevailing current regime, individuals of successive generations would be able to return to the Clyde Sea Area.

5.2.5 Implications for Higher Trophic Levels

The differences in species composition and biomass spectra of the zooplankton faunas throughout the study area may also have implications for the structuring of higher trophic levels within each region. Numerous studies have proposed the existence of alternative food webs, related to factors such as water-column depth (Matthews and Heimdal 1980), degree of mixing (Cushing 1989), and size composition of the primary producers (Cushing 1989; Legendre 1990). In the case of fjords and polls (small fjords with shallow openings), sill depth is also of importance (Matthews and Heimdal 1980).

Cushing (1989) describes the shorter, 'traditional' food web as that of primary producer (> 5μm) to copepods to fish; the alternative food web is microbially based with small, < 5μm primary producers.

Although copepods also form a component of the 'microbial' food web, they tend to be small in size. Because more steps are involved in the transfer of energy from primary producer to higher trophic levels much of the energy may be dissipated before reaching the larger animals (Legendre 1990). Similarly, Landry (1977) proposed that smaller sized assemblages gave rise to medusae and ctenophores while the larger phytoplankton and zooplankton fractions gave rise to fish. This latter food-web is typical of north Norwegian fjords which support a large fishery (Hopkins 1981).

The data available regarding the size composition of primary producers (see section 2.3.2) show that there were differences throughout the study area. A greater proportion of the primary production was comprised by larger phytoplankton in the Firths of Lorn and Clyde than on the Malin Shelf. Correspondingly, smaller copepods were more abundant on the Malin Shelf while larger copepods such as *Calanus* predominated in regions of the Firth of Clyde. Although much of the primary production was in the >5μm fraction in the Firth of Lorn, larger copepods were not common in the firth and this is probably related to the dynamic hydrography of the area.

Differences in food web structure will affect higher trophic levels through the availability of energy channelled through the food web. For fisheries production, of equal importance is the availability of suitable food items for fish larvae upon hatching. Copepod eggs, nauplii and copepodids constitute the main source of food for a large variety of larval fish species (e.g. Arthur 1977; Last 1980; Checkley 1982; Heath *et al.* 1989; Economou 1991). The abundant copepod nauplii and early copepodid stages in the Firth of Clyde during March and May are a potential source of food for larvae of spring spawning fish. The Firth of Clyde has traditionally supported an important herring fishery based on a spring-spawning stock although more recently this has shifted to that based on a population of autumn-spawners (Bailey *et al.* 1986).

The Firth also supports a well developed demersal fishery of predominantly cod, whiting, saithe, hake and haddock (Hislop 1986). All species are thought to spawn locally and the results of tagging experiments suggest that the populations are relatively contained within the region.

In contrast, the Firth of Lorn appears to constitute a nursery ground for juvenile fish rather than a spawning site (e.g. Gordon and De Silva 1980; Gordon 1981; Cooper 1983; Duncan 1991). With the exception of poor-cod which spawn in the region to the south and west of Mull (Cooper 1979, 1983) the presence of whiting and Norway pout in the Firth of Lorn results from an active, inshore migration by 0+ juveniles (Cooper 1980). By the time these fish undertake their inshore migrations, much of the population consists of benthic feeding individuals (Duncan 1991) and therefore will not be dependent on food items distributed throughout the water-column.

Last (1980) found cirripede nauplii in the diets of only three out of twenty species of larval fish examined from the west/central North Sea, although no indication was given regarding how the stomach contents were related to the composition of the plankton during the study. During the spring, cirripede nauplii dominate the zooplankton fauna in the Firth of Lorn and copepod nauplii and early copepodid stages are rare. This suggests that the absence of spawning fish in the Firth is related to the lack of suitable food resources for the larvae. This will not only be related to the overall food web structure as determined by the different size fractions of primary and secondary producers, but also to factors such as the timing and magnitude of the spring phytoplankton bloom and the size of the overwintering zooplankton standing stocks.

6. SUMMARY AND CONCLUSIONS

The results of this study have shown the feasibility of using image analysis in the routine processing of marine zooplankton samples. However, much work is still required in order to develop a fully automated programme for general use in plankton studies. A programme was developed for use in the present study and experiments were conducted in order to examine various aspects of the performance of the image analyser in processing planktonic material. These experiments raised several questions regarding such factors as the selection of length measurements and how variability in discrimination parameters could effect the automation of image analysis programmes.

The results have also shown that over the period of investigation zooplankton assemblages could be identified throughout the study area off the west coast of Scotland. These assemblages differed in terms of species composition and relative abundances, standing stocks, and the partitioning of biomass among species. Overall, assemblages could be related to the different geographical regions, i.e. the Firth of Lorn, Firth of Clyde, and Malin Shelf. However, the results of the multivariate analyses showed there was some variability in station groupings.

Zooplankton numbers and biomass were low in March and high in May, typical of zooplankton assemblages in boreal/temperate waters before and after the spring phytoplankton bloom. Possible differences in the timing of the spring bloom throughout the study area suggested that zooplankton numbers were near maximum in the Firth of Clyde during the May cruise, but possibly not in the Firth of Lorn and on the Malin Shelf.

Results of the multivariate analyses and data on species distribution provided information regarding the structure and composition of zooplankton assemblages throughout the study area. In the Firth of Lorn, the zooplankton assemblage consisted primarily of

meroplankton, small copepods such as *Acartia clausi*, and cladocerans. Resting eggs were thought to be of great importance in the recruitment of zooplankton in the Firth during the spring period.

The Firth of Clyde, in contrast to other regions of the study area, contained a large, resident population of *Calanus finmarchicus*, which overwinters in the deep-waters surrounding Arran, and in Loch Fyne. As a result of the larger-sized *Calanus* populations, zooplankton standing stocks in the Firth of Clyde attained higher levels than were observed in other regions of the study area.

The zooplankton fauna on the Malin Shelf was characterised by small copepods, such as *Oithona* spp., and *Pseudocalanus* spp.. Stations on the shelf were separate from those in the inner Firth of Lorn and the North Channel. This separation corresponded with the presence of the Islay Front which is thought to constitute a faunal barrier.

There also appeared to be potential for the exchange and mixing of zooplankton between regions of the study area. The high standing stocks observed in the Firth of Clyde indicate that this region could be an important source of material for the contiguous coastal waters. The results of the multivariate analyses, in conjunction with the oceanographic observations, suggested that entrainment of material from the Firth of Clyde occurred during the spring when the Scottish Coastal Current has a high rate of flow through the North Channel. The fate of this material is subject to debate, although export is most likely unidirectional.

The Malin Shelf may also constitute a source of zooplankton for the Firth of Lorn. This is thought to be limited to the winter months when an onshore flow of Atlantic water occurs. It is possible that the Malin Shelf provides an important source of material for the Firth of Lorn where conditions appear to be unsuitable for the overwintering of many zooplankton species.

Differences in the structure and composition of the zooplankton

assemblages are also thought to have implications for higher trophic levels. The absence of populations of spawning fish in the Firth of Lorn appears to be related to the lack of suitable food items for the fish larvae. In the Firth of Clyde, where copepod nauplii and copepodids are abundant, several species of fish spawn locally.

This study has provided details of the structure and composition of zooplankton assemblages off the west coast of Scotland, and from these data the potential for the mixing and exchange of planktonic material within the study area has been inferred. Studies examining the effects of advective processes on zooplankton assemblages are always difficult to conduct due to the problem of identifying discrete populations. Levels of zooplankton overwintering standing stocks are also known to be an important factor affecting recruitment success in subsequent spring populations. This will in turn affect the overall production within an area and therefore the potential for exporting planktonic material. Resting eggs are one strategy which may be adopted to enhance recruitment in areas of harsh conditions where overwintering populations are not viable.

The results of this study suggest that material from the Firth of Clyde is entrained by the Scottish Coastal Current during the spring period. However, more detailed studies enabling discrete populations to be identified are required to accurately determine the magnitude and subsequent fate of material advected from the Firth. This also applies to the Malin Shelf as a potential source of material for the Firth of Lorn. In addition, studies are required to determine the composition and standing stocks of zooplankton throughout the study area during the winter period. This would include an investigation into the potential role of resting eggs in zooplankton recruitment within areas such as the Firth of Lorn. Further work in both these areas of research would greatly enhance our knowledge of the longer-term structure and dynamics of zooplankton assemblages in waters off the west coast of Scotland.

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Appendix 1. Cruise data for zooplankton pump samples collected from the study area aboard the R.V. G.A. Reay between 14-25 May 1986. Size fractions are designated as coarse (C, > 1000 µm), medium (M, 1000µm-330 µm) or fine (F, 330 µm-180µm). VWF is the volume of water filtered. For all samples that were subsampled (SS=Y) 1/2 of the sample was preserved, otherwise (SS=N) the entire sample was preserved. Sampleno is a number that was allocated (arbitrarily) to each size fraction during processing. ~ indicates that the time is approximate. * indicates that a CTD dip was not made at the time of collection. All depths are in meters.

DATE (D/M)	PERMANENT STATION NO.	LATITUDE (°N)	LONGITUDE (°W)	BOTTOM DEPTH	CRUISE STATION NO.	CTD DIP NO.	TIME (GMT)	SAMPLING DEPTH	SIZE	VWF (m^3)	SS	SAMPLENO
14.05	FL15	56 28	5 30.5	48	1	3	1530	30	M	1.36	Y	001
									F	1.00	Y	002
							1555	10	M	1.86	Y	003
									F	1.31	Y	004
14.05	FL12	56 14	6 02	87	4	6	2130	30	M	1.54	Y	005
									F	1.20	Y	006
							2155	10	M	2.03	Y	007
									F	1.37	Y	008
15.05	FL12	56 14	6 02	95	4b	12	1500	30	C	1.40	Y	009
									M	1.36	Y	010
									F	1.08	Y	011
							~1530	10	C	2.22	Y	012
									M	1.60	Y	013
									F	1.05	Y	014
16.05	FL8	56 10	6 45	83	12	24	1025	30	C	2.36	N	015
									M	2.07	Y	016
									F/M	1.29	Y	017
16.05	M3	56 10	7 25	110	15	29	1815	30	C	1.64	N	018
									M	1.43	Y	019
									F	1.01	Y	020
							~1845	10	C	1.59	N	021
									M	1.77	Y	022
									F	1.13	Y	023
17.05	FL1	56 10	8 30.3	130	19	33	0900	30	C	2.14	N	024
									M	1.66	Y	025
									F	1.10	Y	026
							~0930	10	M	1.78	Y	027
									F	1.16	Y	028

Appendix 1. Continued

DATE (D/M)	PERMANENT STATION NO.	LATITUDE (°N)	LONGITUDE (°W)	BOTTOM DEPTH	CRUISE STATION NO.	CTD DIP NO.	TIME (GMT)	SAMPLING DEPTH	SIZE	VWF (m^3)	SS	SAMPLENO
18.05	A3	55 13	5 52	128	29	46	0800	30	M	1.46	Y	029
									F	1.05	Y	030
								10	M	0.96	Y	031
									F	0.73	Y	032
18.05	Y5	55 13	5 38	80	32	48	1430	30	C	2.85	N	033
									M	2.19	Y	034
									F	1.00	Y	035
								10	C	2.66	N	036
									C/M	2.14	Y	037
									F	1.00	Y	038
18.05	Y3	55 05	5 26	100	34	52	1730	30	C	1.88	N	039
									M	1.61	Y	040
									F	1.06	Y	041
							~1800	10	C	1.74	N	042
									M	1.71	Y	043
									F	1.06	Y	044
18.05	Y3	55 05	5 26	100	34	*	2110	30	C	1.60	N	045
									M	1.49	N	046
									F/M	1.00	N	047
							2135	10	C	1.51	N	048
									M	1.54	N	049
									F/M	1.00	N	050
19.05	AB3A	55 04	5 16	76	37	54	0150	30	C	1.22	N	051
									M	1.21	Y	052
									F	1.01	Y	053
							0210	10	C	1.81	N	054
									M	1.56	Y	055
									F	0.99	Y	056
19.05	AB8	55 11	5 10	52	44	62	0910	30	C	1.02	N	057
									M	1.71	Y	058
									F/M	0.94	Y	059
								10	C	2.69	N	060
									M	2.41	Y	061
									F/M	1.47	Y	062

Appendix 1. Continued

DATE (D/M)	PERMANENT STATION NO.	LATITUDE (°N)	LONGITUDE (°W)	BOTTOM DEPTH	CRUISE STATION NO.	CTD DIP NO.	TIME (GMT)	SAMPLING DEPTH	SIZE	VWF (m^3)	SS	SAMPLENO
20.05	AB40	55 54	5 23	147	61	81	1545	30	C	1.15	N	069
									M	0.40	Y	070
									F	1.03	Y	071
							1530	10	C	1.67	N	072
									M	0.06	Y	073
									F	1.27	Y	074
20.05	AB38	55 47	5 14	139	64	84	2040	30	C	1.98	N	087
									M	0.38	Y	088
									F/M	1.00	Y	089
							2100	10	C	1.98	N	090
									M	0.63	Y	091
									F/M	1.04	Y	092
21.05	AB30	55 34	4 59	96	60	93	1210	30	C	1.22	N	093
									M	0.08	Y	094
									F	1.02	Y	095
							1230	10	C	1.75	N	096
									M	1.31	Y	097
									F	0.98	Y	098
21.05	AB44	55 42	5 21	127	72	98	1940	30	C	1.06	N	099
									M	1.15	Y	100
									F	0.56	Y	101
							1955	10	C	1.32	N	102
									M	1.20	Y	103
									F	0.66	Y	104
22.05	AB17	55 27	5 28	71	77	103	0050	30	C	1.53	N	105
									M	0.60	Y	106
									F	1.07	Y	107
							0110	10	M	1.09	Y	109
									F	1.01	Y	110
22.05	AB5	55 12	5 27	83	83	109	0755	30	C	1.26	N	111
									M	1.42	Y	112
									F/M	0.71	Y	113
							0820	10	C	2.15	N	114
									M	1.98	Y	115
									F/M	1.17	Y	116

Appendix 1. Concluded.

DATE (D/M)	PERMANENT STATION NO.	LATITUDE (°N)	LONGITUDE (°W)	BOTTOM DEPTH	CRUISE STATION NO.	CTD DIP NO.	TIME (GMT)	SAMPLING DEPTH	SIZE	VWF (m^3)	SS	SAMPLENO
22.05	Z4	54 44	5 15	274	85	111	1530	30	M	1.08	Y	117
									F	0.29	Y	118
							545	10	M	1.05	Y	119
									F	0.75	Y	120
23.05	C3	55 23	6 37	85	89	116	0250	30	M	1.60	Y	121
									F	0.65	Y	122
							0315	10	M	1.06	Y	123
									F	1.06	Y	124
23.05	C6	55 37	6 26	65	92	119	0720	30	M	1.38	Y	125
									F	0.52	Y	126
							0750	10	C	1.29	N	127
									M	1.07	Y	128
									F	0.76	Y	129
24.05	E2	56 08	5 56	75	E2	*	1545	30	M	1.14	Y	158
									F	0.61	Y	159
							1600	10	M	1.28	Y	160
									F	0.64	Y	161

Appendix 2. Cruise data for zooplankton pump samples collected from the study area aboard the R.R.S. Frederick Russell between 19-27 March 1987. Size fractions are designated as coarse (C, > 1000 μm), medium (M, 1000 μm-330 μm) or fine (F, 330 μm-180 μm). VWF is the volume of water filtered. For all samples that were subsampled (SS=Y) 1/2 of the sample was preserved, otherwise (SS=N) the entire sample was preserved. Sampleno is a number that was allocated (arbitrarily) to each size fraction during processing. ~ indicates that the time is approximate. * indicates that a CTD dip was not made at the time of collection. All depths are in m.

DATE (D/M)	PERMANENT STATION NO.	LATITUDE (°N)	LONGITUDE (°W)	BOTTOM DEPTH	CRUISE STATION NO.	CTD DIP NO.	TIME (GMT)	SAMPLING DEPTH	SIZE	VWF (m^3)	SS	SAMPLENO
20.03	AB44	55 42	5 21	110	6	6	0300	30	M	1.01	Y	309
									F	0.69	Y	310
							~0315	10	M	1.18	Y	311
									F	0.77	Y	312
20.03	AB38	55 47	5 14	156	9	9	0729	30	M	1.02	Y	313
									F	0.68	Y	314
							0745	10	M	1.12	Y	315
									F	0.78	Y	316
20.03	AB38A	55 50	5 11	59	10	10	0945	30	M	1.09	Y	317
									F	0.67	Y	318
							1000	10	M	1.28	Y	319
									F	0.89	Y	320
20.03	AB40	55 54	5 23	144	12	12	1350	30	M	1.02	Y	321
									F	0.68	Y	322
							~1405	10	M	1.16	Y	323
									F	0.77	Y	324
20.03	AB34	55 50	4 55	67	16	16	2140	30	M	1.01	Y	325
									F	0.66	Y	326
							2155	10	M	1.05	Y	327
									F	0.79	Y	328
21.03	AB35A	55 53.5	5 04	56	18	18	0015	30	M	1.06	Y	329
									F	0.86	Y	330
							0030	10	M	1.04	Y	331
									F	0.80	Y	332
21.03	AB30	55 34	4 59	99	28	28	1150	30	M	1.14	Y	333
									F	0.81	Y	334
							~1205	10	M	1.36	Y	335
									F	1.13	Y	336

Appendix 2. Continued

DATE (D/M)	PERMANENT STATION NO.	LATITUDE (°N)	LONGITUDE (°W)	BOTTOM DEPTH	CRUISE STATION NO.	CTD DIP NO.	TIME (GMT)	SAMPLING DEPTH	SIZE	VWF (m^3)	SS	SAMPLENO
21.03	AB28	55 28	4 45	44	30	30	1540	30	M	1.00	Y	337
									F	0.74	Y	338
							~1555	10	M	1.06	Y	339
									F	0.75	Y	340
21.03	AB25	55 29	5 01	102	33	33	1945	30	M	1.10	Y	341
									F	0.87	Y	342
							~1950	10	M	0.99	Y	343
									F	0.64	Y	344
22.03	AB22	55 16	4 56	36	38	38	0300	30	M	1.01	Y	349
									F	0.61	Y	350
							~0315	10	M	1.04	Y	351
									F	0.72	Y	352
22.03	AB20	55 20	5 08	56	40	40	0910	30	M	1.01	Y	353
									F	0.77	Y	354
							0925	10	M	1.06	Y	355
									F	0.71	Y	356
22.03	AB14	55 19	5 20	46	43	43	1330	30	M	1.51	Y	357
									F	1.02	Y	358
							~1345	10	M	1.02	Y	359
									F	0.76	Y	360
22.03	AB8	55 11	5 10	52	49	49	2015	30	M	1.06	Y	361
									F	0.68	Y	362
							2030	10	M	1.01	Y	363
									F	0.70	Y	364
22.03	AB5	55 12	5 27	73	52	52	2325	30	M	1.00	Y	365
									F	0.61	Y	366
							2335	10	M	1.00	Y	367
									F	0.69	Y	368
23.03	AB1	55 05	5 04	20	56	56	0345	10	M	1.02	Y	369
									F	0.71	Y	370
23.03	AB3A	55 04	5 16	75	57	57	0530	30	M	1.00	Y	371
									F	0.59	Y	372
							0544	10	M	1.00	Y	373
									F	0.80	Y	374

Appendix 2. Continued

DATE (D/M)	PERMANENT STATION NO.	LATITUDE (°N)	LONGITUDE (°W)	BOTTOM DEPTH	CRUISE STATION NO.	CTD DIP NO.	TIME (GMT)	SAMPLING DEPTH	SIZE	VWF (m^3)	SS	SAMPLENO
23.03	Y1	54 57	5 14	54	58	58	~0700	30	M	1.00	Y	375
									F	0.52	Y	376
							~0720	10	M	0.99	Y	377
									F	0.53	Y	378
23.03	Z4	54 44	5 15	253	61	61	1205	30	M	1.01	Y	379
									F	0.75	Y	380
							~1220	10	M	1.02	Y	381
									F	0.73	Y	382
23.03	Y3	55 05	5 26	96	65	65	1840	30	M	0.99	Y	383
									F	0.69	Y	384
							1845	10	M	1.00	Y	385
									F	0.69	Y	386
23.03	AB15	55 20	5 28	50	68	68	2220	30	M	1.02	Y	387
									F	0.71	Y	388
							2235	10	M	1.00	Y	389
									F	0.68	Y	390
24.03	AB17	55 27	5 28	62	70	70	0020	30	M	0.97	Y	391
									F	0.62	Y	392
							~0035	10	M	1.04	Y	393
									F	0.65	Y	394
24.03	A2	55 15	5 47	120	72	72	0432	30	M	1.02	Y	395
									F	0.65	Y	396
							0445	10	M	1.00	Y	397
									F	0.66	Y	398
24.03	A4	55 11	5 56	137	74	74	0700	30	M	1.00	Y	399
									F	0.56	Y	3100
							0720	10	M	1.00	Y	3101
									F	0.62	Y	3102
24.03	C3	55 23	6 37	80	78	78	1701	30	M	1.00	Y	3103
									F	0.64	Y	3104
							~1716	10	M	1.00	Y	3105
									F	0.56	Y	3106
24.03	C5	55 32	6 30	100	80	80	1940	30	M	1.00	Y	3107
									F	0.65	Y	3108
							1955	10	M	1.00	Y	3109
									F	0.92	Y	3110

Appendix 2. Concluded.

DATE (D/M)	PERMANENT STATION NO.	LATITUDE (°N)	LONGITUDE (°W)	BOTTOM DEPTH	CRUISE STATION NO.	CTD DIP NO.	TIME (GMT)	SAMPLING DEPTH	SIZE	VWF (m^3)	SS	SAMPLENO
24.03	D7	55 46	6 37	60	83	83	2335	30	M	1.00	Y	3111
									F	0.66	Y	3112
							2345	10	M	1.00	Y	3113
									F	0.70	Y	3114
25.03	D4	55 46	7 04	45	86	86	0315	30	M	1.04	Y	3115
									F	0.64	Y	3116
							~0330	10	M	0.98	Y	3117
									F	0.55	Y	3118
25.03	D0	55 46	8 00	101	90	90	1035	30	M	1.00	Y	3119
									F	0.59	Y	3120
							1050	10	M	1.00	Y	3121
									F	0.73	Y	3122
25.03	FL0	56 10	8 45	124	91	91	1620	30	M	0.99	Y	300
									F	0.78	Y	301
							1640	10	M	0.99	Y	302
									F	0.71	Y	303
26.03	FL9	56 10	6 30	55	100	100	0840	30	M	1.00	Y	3123
									F	0.64	Y	3124
							0855	10	M	1.12	Y	3125
									F	0.66	Y	3126
26.03	FL12	56 14	6 02	75	103	103	1405	30	M	1.30	Y	3131
									F	0.87	Y	3132
							~1420	10	M	0.99	Y	3133
									F	0.70	Y	3134
26.03	FL13	56 17	5 50	130	109	109	2200	30	M	1.00	Y	3139
									F	0.69	Y	3140
							2215	10	M	1.00	Y	3141
									F	0.71	Y	3142
27.03	FL15	56 28	5 30	45	111	111	0130	30	M	1.03	Y	3143
									F	0.70	Y	3144
							~0145	10	M	1.03	Y	3145

Appendix 3. Results from the second zooplankton sample examined to evaluate the performance of the subsampling device. Each subsample (SS1 to SS3) represents 1/4 of the total sample. $\tilde{N}$ is the population estimate based on the three subsamples. N is the total number for the whole sample. $\bar{x}$ is the mean value per three subsamples. s is the standard deviation. CV is the coefficient of variation (100·(s/x)); - indicates value could not be calculated. Taxa are arranged according to increasing coefficients of variation.

Species	SS1	SS2	SS3	$\bar{x}$	$\tilde{N}$	N	s	CV
Echinoderm larvae	1	1	1	1.00	4.00	3	0.00	0
Calanus spp.	43	53	41	45.67	182.67	186	6.43	14
Cirripede nauplii	9	12	14	11.67	46.67	47	2.52	22
Pseudocalanus spp.	3	1	3	2.33	9.33	8	1.15	49
Temora longicornis	1	3	3	2.33	9.33	7	1.15	49
Unidentified copepodid	1	2	3	2.00	8.00	6	1.00	50
Thysanoessa raschii	4	1	3	2.67	10.67	10	1.53	57
Acartia clausi	1	1	0	0.67	2.67	2	0.58	87
Calanus finmarchicus	2	0	2	1.33	5.33	6	1.15	87
Evadne nordmanni	1	0	1	0.67	2.67	2	0.58	87
Oithona spp.	0	0	1	0.33	1.33	1	0.58	173
Polychaete larvae	0	0	1	0.33	1.33	2	0.58	173
Meganyctiphanes norvegica	1	0	0	0.33	1.33	1	0.58	173
Copepod nauplii	0	1	0	0.33	1.33	1	0.58	173
Cyprid	0	0	1	0.33	1.33	1	0.58	173
Centropages hamatus	0	1	0	0.33	1.33	1	0.58	173
Euphausiid nauplii	0	1	0	0.33	1.33	3	0.58	173
Euphausiid eggs	1	0	0	0.33	1.33	3	0.58	173
Galatheid zoeae	0	0	0	0.00	0.00	1	0.00	-

Appendix 4. Results from the third zooplankton sample examined to evaluate the performance of the subsampling device. Each subsample (SS1 to SS3) represents 1/4 of the total sample. $\tilde{N}$ is the population estimate based on the three subsamples. N is the total number for the whole sample. $\bar{x}$ is the mean value per three subsamples. s is the standard deviation. CV is the coefficient of variation ($100 \cdot (s/x)$); - indicates value could not be calculated. Taxa are arranged according to increasing coefficients of variation.

Species	SS1	SS2	SS3	$\bar{x}$	$\tilde{N}$	N	s	CV
Cirripede nauplii	9	8	7	8.00	32.00	32	1.00	13
Thysanoessa raschii	3	2	2	2.33	9.33	9	0.58	25
Calanus spp.	25	12	21	19.33	77.33	85	6.66	34
Temora longicornis	2	2	1	1.67	6.67	6	0.58	35
Copepod nauplii	0	1	1	0.67	2.67	4	0.58	87
Euphausiid nauplii	1	1	0	0.67	2.67	3	0.58	87
Centropages hamatus	1	1	0	0.67	2.67	5	0.58	87
Pseudocalanus spp.	1	1	0	0.67	2.67	3	0.58	87
Echinoderm larvae	1	0	2	1.00	4.00	3	1.00	100
Caridean zoeae	0	1	0	0.33	1.33	1	0.58	173
Meganyctiphanes norvegica	0	1	0	0.33	1.33	1	0.58	173
Acartia clausi	0	2	0	0.67	2.67	2	1.15	173
Appendicularians	0	0	4	1.33	5.33	4	2.31	173
Euphausiid eggs	0	0	1	0.33	1.33	2	0.58	173
Evadne nordmanni	0	0	1	0.33	1.33	1	0.58	173
Gastropod larvae	0	0	1	0.33	1.33	1	0.58	173
Unidentified eggs	0	0	0	0.00	0.00	1	0.00	-
Unidentified nauplii	0	0	0	0.00	0.00	1	0.00	-
Electra pilosa	0	0	0	0.00	0.00	1	0.00	-

Appendix 5. Results from the fourth zooplankton sample examined to evaluate the performance of the subsampling device. Each subsample (SS1 to SS3) represents 1/4 of the total sample. $\tilde{N}$ is the population estimate based on the three subsamples. N is the total number for the whole sample. $\bar{x}$ is the mean value per three subsamples. s is the standard deviation. CV is the coefficient of variation ($100 \cdot (s/x)$); - indicates value could not be calculated. Taxa are arranged according to increasing coefficients of variation.

Species	SS1	SS2	SS3	$\bar{x}$	$\tilde{N}$	N	s	CV
Pseudocalanus spp.	6	7	5	6.00	24.00	25	1.00	17
Calanus finmarchicus	2	3	2	2.33	9.33	8	0.58	25
Calanus spp.	19	18	12	16.33	52.00	48	5.57	43
Temora longicornis	8	7	3	6.00	24.00	26	2.65	44
Evadne nordmanni	1	3	2	2.00	8.00	8	1.00	50
Acartia clausi	7	6	2	5.00	20.00	16	2.65	53
Oithona spp.	1	0	1	0.67	2.67	2	0.58	87
Microcalanus spp.	0	0	1	0.33	1.33	1	0.58	173
Unidentified	0	1	0	0.33	1.33	1	0.58	173
Bivalve larvae	0	1	0	0.33	1.33	2	0.58	173
Centropages hamatus	0	0	2	0.67	2.67	3	1.15	173
Sagitta spp.	0	0	2	0.67	2.67	3	1.15	173
Euphausiid furcilia	0	0	1	0.33	1.33	1	0.58	173
Unidentified nauplii	0	0	1	0.33	1.33	1	0.58	173
Prosobranch larvae	0	1	0	0.33	1.33	1	0.58	173
Paracalanus parvus	1	0	0	0.33	1.33	1	0.58	173
Cyprid	1	0	0	0.33	1.33	1	0.00	173
Appendicularians	1	0	0	0.33	1.33	1	0.00	173
Tomopteris helgolandica	0	2	0	0.67	2.67	2	1.15	173
Oithona similis	0	1	0	0.33	1.33	1	0.58	173
Anomalocera patersoni	0	0	0	0.00	0.00	1	0.00	-
Podon leuckarti	0	0	0	0.00	0.00	1	0.00	-
Asterioid larvae	0	0	0	0.00	0.00	1	0.00	-
Unidentified copepodids	0	0	0	0.00	0.00	1	0.00	-

Appendix 6. Results from the fifth zooplankton sample examined to evaluate the performance of the subsampling device. Each subsample (SS1 to SS3) represents 1/4 of the total sample. $\tilde{N}$ is the population estimate based on the three subsamples. N is the total number for the whole sample. $\bar{x}$ is the mean value per three subsamples. s is the standard deviation. CV is the coefficient of variation ($100 \cdot (s/x)$); - indicates value could not be calculated. Taxa are arranged according to increasing coefficients of variation.

Species	SS1	SS2	SS3	$\bar{x}$	$\tilde{N}$	N	s	CV
Calanus spp.	23	29	19	23.67	94.67	86	5.03	21
Calanus finmarchicus	16	24	24	21.33	85.33	82	4.62	22
Acartia clausi	7	3	12	10.67	29.33	26	4.51	61
Pseudocalanus spp.	1	0	1	0.67	2.67	3	0.58	87
Oithona spp.	0	1	2	1.00	4.00	3	1.00	100
Unidentified copepodids	0	1	2	1.00	4.00	4	1.00	100
Unidentified eggs	1	0	0	0.33	14.67	11	5.51	150
Nephrops norvegicus	0	1	0	0.33	1.33	1	0.58	173
Temora longicornis	1	0	0	0.33	1.33	1	0.58	173
Centropages hamatus	0	0	3	1.00	4.00	3	1.73	173
Brachyuran zoeae	0	1	0	0.33	1.33	1	0.58	173
Bivalve larvae	1	0	0	0.33	1.33	1	0.58	173
Galatheid zoeae	1	0	0	0.33	1.33	1	0.58	173
Anomalocera patersoni	0	0	1	0.33	1.33	1	0.58	173

Appendix 7. Results from the sixth zooplankton sample examined to evaluate the performance of the subsampling device. Each subsample (SS1 to SS3) represents 1/4 of the total sample. $\bar{N}$ is the population estimate based on the three subsamples. N is the total number for the whole sample. $\bar{x}$ is the mean value per three subsamples. s is the standard deviation. CV is the coefficient of variation ($100 \cdot (s/x)$); - indicates value could not be calculated. Taxa are arranged according to increasing coefficients of variation.

Species	SS1	SS2	SS3	$\bar{x}$	$\bar{N}$	N	s	CV
Microcalanus spp.	27	19	36	27.33	109.33	115	8.50	31
Oithona spp.	9	11	5	8.33	33.33	30	3.06	37
Cirripede nauplii	1	2	1	1.33	5.33	4	0.58	43
Acartia clausi	1	1	3	1.67	6.67	6	1.15	69
Copepod nauplii	6	1	3	3.33	13.33	12	2.52	75
Calanus spp.	5	3	15	7.67	30.67	37	6.43	84
Temora longicornis	1	0	1	0.67	2.67	2	0.58	87
Euphausiid nauplii	1	1	5	2.33	9.33	7	2.31	99
Unidentified eggs	0	0	1	0.33	1.33	1	0.58	173
Unidentified copepodids	0	0	1	0.33	1.33	1	0.58	173
Polychaete larvae	0	0	6	2.00	8.00	7	3.46	173
Membranipora membranacea	1	0	0	0.33	1.33	1	0.58	173
Appendicularians	0	0	2	0.67	2.67	3	1.15	173
Oithona similis	1	0	0	0.33	1.33	2	0.58	173
Bivalve larvae	0	0	0	0.00	0.00	2	0.00	173
Podon leuckarti	0	0	0	0.00	0.00	1	0.00	173
Electra pilosa	0	0	0	0.00	0.00	1	0.00	173

Appendix 8. Image analysis programme used in the present study. For full details of all parameters consult the manual: IBAS 2000 Automatic Measuring Program Description (Kontron Bildanalyse 1985).

FUNCTION	VARIABLES INTEGER		LOGICAL	REAL
1 SYNC				
2 AVERNI				
	INP	12		
	AUX1	13		
	AUX2	14		
	NADD	10		
	NDIV	10		
3 MEDIAN				
	INP	12		
	OUT	13		
	SIZE	5		
	RANK	13		
4 SHDEF				
	INP	13		
	SHRF	14		
5 SCALE				
	SCNO	12	NEW	
6 ID. NO				
	NO	1	EDIT	
7 LAB:				
	LBL£	2		
8 SETVAR				
	——$	1		
	VAL	1		
9 SETVAR	——$	3		
	VAL	1		
10 PAUSE				
11 COPYIM				
	INP	14		
	OUT	11		
12 LAB:				
	LBL£	3		
13 CLEAR				
	INP	3		
	PHAS	255		
	MODE	1		
14 PAUSE				
15 TVON				
			ONLINE	
16 TVINP				
	INP	1		
17 SHADE				
	INP	1		
	OUT	2		
	SHRF	14		
	OFFS	0		

Appendix 8. Continued

FUNCTION	INTEGER VARIABLES		LOGICAL	REAL	
18 EDIT					
	INP	2			
	OUT	2			
	AUX	4			
19 NORMGR					
	INP	2			
	OUT	3			
	THRS	0			
20 ENHCON					
	INP	3			
	OUT	4			
	TYPE	3			
	STRG	1			
21 DELIN					
	INP	4			
	OUT	5			
	LEVEL	155			
	SIZE	5			
22 COPYIM					
	INP	5			
	OUT	4			
23 CLEAR					
	INP	13	ALL		
	PHAS	255			
	MODE	1			
24 PAUSE					
25 DISC2L					
	INP	4	BINARY		
	OUT	5			
	LEV1	(set interactively)			
	LEV2	(set interactively)			
26 DISC2L					
	INP	4	BINARY		
	OUT	6			
	LEV1	(set interactively)			
	LEV2	(set interactively)			
27 SUB					
	INP	5			
	OUT	7			
	INP2	6			
	NRMD	2			
28 AFILL					
	INP	7			
	OUT	8			
29 OPEN					
	INP	8			
	OUT	9			
	PHAS	255			
	CNT	1			
	MODE	7			
30 AREA					
	NCLS	10	SINGLE	LOW	.1000E-01
	MODX	1		HIGH	.1800
	MODY	1			

Appendix 8. Continued

FUNCTION	INTEGER		VARIABLES LOGICAL	REAL	
31 IDENT					
	INP	9	8-CONN		
	OUT	12			
	MARG	0			
32 MS/SKIP					
	INP	12	SKIP		
	OUT	10			
	GRIM	0	OBJ		
33 DISC2L					
	INP	10	BINARY		
	OUT	13			
	LEV1	(set interactively)			
	LEV2	(set interactively)			
34 PAUSE					
35 DISC2L					
	INP	4	BINARY		
	OUT	5			
	LEV1	47			
	LEV2	255			
36 DISC2L					
	INP	4	BINARY		
	OUT	6			
	LEV1	(set interactively)			
	LEV2	(set interactively)			
37 SUB					
	INP	5			
	OUT	7			
	INP2	6			
	NRMD	2			
38 AFILL					
	INP	7			
	OUT	8			
39 OPEN					
	INP	8			
	OUT	7			
	PHAS	255			
	CNT	1			
	MODE	7			
40 AREA	NCLS	10	SINGLE	LOW	.1500
	MODX	1		HIGH	.7500
	MODY	1			
41 IDENT					
	INP	7	8-CONN		
	OUT	8			
	MARG	0			
42 MS/SKIP					
	INP	8	SKIP		
	OUT	9			
	GRIM	0	OBJ		
43 DISC2L					
	INP	9	BINARY		
	OUT	10			
	LEV1	(set interactively)			
	LEV2	(set interactively)			

Appendix 8. Continued

FUNCTION	INTEGER	VARIABLES LOGICAL	REAL
44 ADD			
	INP 10		
	OUT 12		
	INP2 13		
	NRMD 2		
45 PAUSE			
46 DISC2L	INP 4	BINARY	
	OUT 5		
	LEV1 57		
	LEV2 255		
47 DISC2L			
	INP 4	BINARY	
	OUT 6		
	LEV1 (set interactively)		
	LEV2 (set interactively)		
48 SUB			
	INP 5		
	OUT 7		
	INP2 6		
	NRMD 2		
49 AFILL			
	INP 7		
	OUT 8		
50 ERODE			
	INP 8		
	OUT 6		
	PHAS 255		
	CNT 4		
	MODE 7		
51 DILATE			
	INP 6		
	OUT 7		
	PHAS 255		
	CNT 4		
	MODE 7		
52 AREA			
	NCLS 10	SINGLE	LOW .5000
	MODX 1		HIGH 10000.0
	MODY 1		
53 IDENT			
	INP 7	8-CONN	
	OUT 8		
	MARG 0		
54 MS/SKIP			
	INP 8	SKIP	
	OUT 9		
	GRIM 0	OBJ	
55 DISC2L			
	INP 9	BINARY	
	OUT 10		
	LEV1 (set interactively)		
	LEV2 (set interactively)		

Appendix 8. Continued

FUNCTION	INTEGER		VARIABLES LOGICAL	REAL	
56 ADD					
	INP	10			
	OUT	7			
	INP2	12			
	NRMD	2			
57 EDIT					
	INP	7			
	OUT	7			
	AUX	5			
58 CONTUR					
	INP	7	OVLAY		
	OUT	3			
	PHAS	255			
	PHCO	100			
	MODE	2			
59 PAUSE					
60 AREA					
	NCLS	10	SINGLE	LOW	0.000
	MODX	1		HIGH	1000.0
	MODY	1			
61 MOMENT					
	NCLS	10	SINGLE	LOW	0.000
	MODX	1		HIGH	1000.0
	MODY	1	SNGL.Y	LO.Y	0.000
	NCLY	10		HI.Y	1000.0
	MDYX	1			
	MDYY	1			
62 IDENT					
	INP	7	8-CONN		
	OUT	10			
	MARG	0			
63 PAUSE					
64 MEASUR					
	INP	10			
	GRIM	0			
	AUX1	7	OBJ		
	AUX2	7			
	CHAN	10			
	SPAC	1			
	FLGE	1			
65 LUTAB					
	SEL	2			
66 ZOOM					
	INP	2			
	OUT	11			
	$1	5			
	X0	0			
	Y0	0			
67 VAR+C					
	——$	1			
	VAL	1			

Appendix 8. Continued

FUNCTION	INTEGER		VARIABLES LOGICAL	REAL
68 LOOP				
	LBL£	3		
	$3	1		
	TOTL	4		
69 DISPLY				
	INP	11		
70 PAUSE				
71 STORIM				
	INP	11	TITLE	
	$2	1		
72 VAR+C				
	——$	2		
	VAL	1		
73 GOTO				
	LBL£	2		
74 OUTSGL			/	
			STORE	
			PRINT	
75 PAUSE				
76 DISC2L				
	INP	4	BINARY	
	OUT	5		
	LEV1	(set interactively)		
	LEV2	(set interactively)		
77 DISC2L				
	INP	4	BINARY	
	OUT	6		
	LEV1	(set interactively)		
	LEV2	(set interactively)		
78 SUB				
	INP	5		
	OUT	7		
	INP2	6		
	NRMD	2		
79 AFILL				
	INP	7		
	OUT	8		
80 OPEN				
	INP	8		
	OUT	9		
	PHAS	255		
	CNT	1		
	MODE	6		
81 EDIT				
	INP	9		
	OUT	9		
	AUX	5		

Appendix 8. Concluded.

FUNCTION	INTEGER		VARIABLES LOGICAL	REAL
82 CONTUR				
	INP	9	OVLAY	
	OUT	2	LARGE	
	PHAS	255		
	PHCO	100		
	MODE	1		
83 PAUSE				
84 COPYIM				
	INP	9		
	OUT	7		
85 JUMP				
	STEP	-25		
86 PAUSE				
TOTAL PROGRAM LENGTH		1182 BYTES		

Appendix 9. Total zooplankton numbers and biomass for all stations examined at 10m and 30m in May 1986, and the partitioning according to the different size fractions collected: coarse, C; medium, M; fine, F. - denotes that the sample fraction was not collected. ? denotes that the sample fraction could not be accurately measured due to problems that occurred at the time of collection (see section 3.4.2). N and D denote night and day samples collected at the same station. Times of collection for all other stations may be obtained from Appendix 1.

Station	Depth (m)	Number m^{-3}			Total	Biomass ml m^{-3}			Total
		C	M	F		C	M	F	
FL15	10	–	1069	678	1747	–	0.18	0.05	0.23
	30	–	566	1680	2246	–	0.10	0.10	0.20
FL12(N)	10	–	303	860	1163	–	0.10	0.13	0.23
	30	–	297	973	1270	–	0.16	0.07	0.23
FL12(D)	10	4	61	192	257	0.02	0.06	0.06	0.14
	30	50	250	298	598	0.10	0.04	0.09	0.23
FL8	30	9	4782	10688	15479	<0.01	2.44	1.52	3.96
M3	10	11	2242	3153	5406	0.02	2.75	3.58	6.35
	30	32	1029	4499	5560	0.01	0.31	0.42	0.74
FL1	10	–	520	9747	10267	–	0.02	0.52	0.54
	30	13	490	5896	6399	<0.01	0.14	1.84	1.98
A3	10	–	639	2594	3233	–	0.15	0.11	0.26
	30	–	1182	4653	5840	–	0.19	2.67	2.86
Y5	10	5	2268	2667	4940	<0.01	2.24	3.76	6.00
	30	4	1047	3829	4880	<0.01	0.21	0.20	0.41
Y3(D)	10	29	1235	4166	5430	0.02	0.14	0.44	0.60
	30	46	2703	4589	7338	0.07	2.66	0.75	3.48
Y3(N)	10	105	2854	4719	7678	0.09	1.62	0.58	2.29
	30	32	1976	5399	7407	0.02	1.42	0.80	2.24
AB3A	10	2	735	5150	5887	0.02	0.36	0.16	0.54
	30	10	1463	3718	5191	0.01	0.12	0.40	0.53
AB8	10	6	1124	1504	2634	0.01	1.54	?	1.55
	30	13	689	2588	3290	0.02	0.10	0.40	0.52
AB40	10	128	787911	32521	820560	0.22	374.00	17.51	391.73
	30	23	2440	1067	3530	0.04	2.05	0.31	2.40
AB38	10	46	22214	2927	25187	0.04	12.32	?	12.36
	30	28	8786	915	9729	0.04	12.55	?	12.59
AB30	10	18	4250	4376	8644	0.03	3.43	4.76	8.22
	30	13	32667	2614	5894	0.02	50.62	3.66	54.30
AB44	10	43	13653	11248	24944	0.04	10.15	8.59	18.78
	30	17	1370	1824	3211	0.08	0.98	0.66	1.72
AB17	10	–	5598	8660	14258	–	4.91	4.76	9.67
	30	7	16782	6191	22980	0.20	6.42	5.20	11.82
AB5	10	35	1476	3435	4946	0.04	0.17	2.85	3.06
	30	10	2254	4740	7004	0.08	0.42	0.10	0.60
Z4	10	–	3550	13312	16862	–	1.50	0.84	2.34
	30	–	4820	24938	29758	–	0.85	2.74	3.59
C3	10	–	223	672	895	–	0.18	0.14	0.32
	30	–	450	2068	2518	–	0.12	0.14	0.26
C6	10	9	290	1979	2278	0.01	0.04	0.12	0.17
	30	–	485	4903	5388	–	0.10	0.10	0.20
E2	10	–	72	203	275	–	0.94	0.94	1.88
	30	–	135	459	594	–	0.09	0.20	0.29

Appendix 10. Total zooplankton numbers and biomass for all stations examined at 10m and 30m in March 1987, and the partitioning according to the different size fractions collected: medium, M; fine, F. Information regarding sample collection can be found in Appendix 2.

Station	Depth (m)	Number m^{-3}		Total	Biomass ml m^{-3}		Total
		M	F		M	F	
FL15	10	31	171	202	0.08	0.14	0.22
	30	16	814	830	0.04	0.23	0.27
FL13	10	84	1063	1147	0.10	0.08	0.18
	30	192	2133	2325	0.16	0.29	0.45
FL12	10	69	783	852	0.12	0.23	0.35
	30	58	769	827	0.11	0.07	0.18
FL9	10	84	1584	1668	0.11	0.12	0.23
	30	158	2458	2616	0.14	0.16	0.30
FL0	10	36	225	261	0.06	0.03	0.09
	30	30	236	266	0.06	0.03	0.09
D0	10	78	482	560	0.24	0.25	0.49
	30	82	512	594	0.20	0.17	0.37
D4	10	76	1746	1822	0.18	0.33	0.51
	30	58	2250	2308	0.12	0.09	0.21
D7	10	56	694	750	0.14	0.17	0.31
	30	104	1036	1140	0.18	0.15	0.33
A2	10	262	252	514	0.20	0.18	0.38
	30	198	243	441	0.35	0.18	0.53
A4	10	42	71	113	0.18	0.26	0.44
	30	62	275	337	0.16	0.25	0.41
C3	10	40	400	440	0.06	0.25	0.31
	30	64	94	158	0.12	0.03	0.15
C5	10	110	307	417	0.24	0.13	0.37
	30	80	89	169	0.18	0.09	0.27
Y1	10	160	758	918	0.24	0.15	0.39
	30	284	581	865	0.20	0.15	0.35
Y3	10	162	959	1121	0.22	0.12	0.34
	30	176	319	495	0.08	0.06	0.14
Z4	10	37	334	371	0.12	0.22	0.34
	30	81	335	436	0.08	0.11	0.19
AB1	10	429	1788	2217	0.12	0.11	0.23
AB14	10	2290	2537	4827	0.39	0.18	0.57
	30	2352	2416	4768	1.36	0.17	1.53
AB15	10	386	1482	1868	0.18	0.21	0.39
	30	265	783	1048	0.29	0.23	0.52
AB20	10	413	2378	2791	0.13	0.11	0.24
	30	600	1822	2422	0.16	0.23	0.39
AB22	10	227	2533	2810	0.12	0.14	0.26
	30	246	944	1190	0.16	0.16	0.32
AB25	10	473	1371	1844	0.26	0.34	0.60
	30	453	349	802	0.22	0.16	0.38
AB3A	10	152	400	552	0.12	0.10	0.22
	30	190	1139	1329	0.10	0.14	0.24
AB5	10	108	365	473	0.16	0.20	0.36
	30	148	731	879	0.16	0.20	0.36
AB8	10	329	2366	2695	0.06	0.09	0.15
	30	553	1288	1841	0.11	0.15	0.26

Appendix 10. Concluded.

Station	Depth (m)	Number m^{-3}		Total	Biomass ml m^{-3}		Total
		M	F		M	F	
AB28	10	2583	1184	3767	0.34	0.32	0.66
	30	368	987	1355	0.36	0.24	0.60
AB30	10	94	540	634	0.07	0.12	0.19
	30	116	1027	1143	0.12	0.17	0.29
AB34	10	2672	7264	9936	0.34	0.48	0.82
	30	259	1479	1738	0.16	0.30	0.46
AB35A	10	427	490	917	0.23	0.20	0.43
	30	519	1383	1902	0.23	0.23	0.46
AB38	10	66	146	212	0.11	0.18	0.29
	30	75	21	96	0.20	0.24	0.44
AB38A	10	125	884	1009	0.14	0.20	0.34
	30	290	1128	1418	0.15	0.33	0.48
AB40	10	28	203	231	0.07	0.16	0.23
	30	69	288	357	0.25	0.26	0.51
AB17	10	1019	1440	2459	0.35	0.15	0.50
	30	532	677	1209	0.39	0.26	0.65
AB44	10	217	231	448	0.10	0.13	0.23
	30	1067	672	1739	0.16	0.09	0.25