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A review of biological processes within oceanic water columns relevant to the assessment of the safety of disposal of waste, notably radioactive isotopes on or within the seabed.

M.V. Angel

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NATURAL ENVIRONMENT RESEARCH COUNCIL

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Abstract

Pelagic biological processes and their connotations in the assessment of possible dispersal mechanisms of contaminants released on the deep oceanic seabed are reviewed. Biological gradients tend to be from the surface down so the search is for processes which run counter to these general gradients. Observed profiles of standing crop of both plankton and micronekton show that below 2000m biological activity would have to be exceptionally dynamic to have an influence that will even approach within an order of magnitude of the dispersive effect of physical mixing. Examination of all forms of known migration mechanisms fails to reveal such dynamic activity. Nor have any critical pathways been identified within the present or foreseeable pattern of exploitation of the oceans. However, a major gap in knowledge is whether the pattern of these biological processes changes substantially in the region of continental slopes.

Keywords
299 , 148, 153, 154, 155

CONTENTS

INTRODUCTION

This review seeks to outline biological processes in the water column making particular reference to the work that has been conducted by the biology department at IOS over the last one and a half decades in the Northeast Atlantic. It will provide references and where necessary fuller descriptions of results from the scientific literature, in order to provide the reader with a general insight into the processes. Then the connotations of the available data and modern hypotheses will be discussed in the context of the problems associated with assessment of the environmental and radiological safety of any existing or potential programme for disposal of waste substances, especially radioactive isotopes on or within the seabed.

Any such assessment must explore how the effects of any disposal can be minimised so that it remains within the 'carrying capacity' of the ecosystem. In the GESAMP Report No. 15 it was stated that:- "The disposal of waste at sea can be scientifically discussed without attempting to justify the operation. The concept of a capacity of the oceans to receive waste has long been accepted and utilized by mankind, though the criteria of assimilative capacity have not been static. Early criteria tended to be based on visual or aesthetic factors .... More recently the potential effects of persistent and toxic wastes on the health and stability of the ecosystem and on its human users have been highlighted. In accepting that the marine environment has a capacity to receive wastes, it must be recognised that this is often largely related to the great volume of the oceans; that the self-purification and buffering capacity of the water is limited, and that the sea-bed will not act as an effective sink for all materials or for infinite amounts."

An additional concern that is of particular importance in the disposal of radioactive wastes, but is by no means restricted to this class of substances, is to ascertain that any slight traces, which may be returned via a variety of pathways either to the total human population or to critical groups, do not constitute a health hazard in either the long or short-term. In the seabed disposal of low-level waste the approach has been to render the radioactive material relatively immobile and then to rely on the dilution and dispersion effects of the oceans to prevent the build up of any of the isotopes in sufficient quantities to create any significant hazard.

The proposed strategy for the disposal of high-level waste in the seabed is based on the concept of multiple barriers. The initial barrier consists of the specially engineered canister into which the waste is cast incorporated into some inert form such as a boro-silicate glass. Design criteria set for the canisters aim at their integrity being maintained in deep oceanic environments for at least 1000 years. The second barrier will be the stable sedimentary layers beneath which the canisters will be buried either within specially engineered boreholes or by designing the canisters as free-fall penetrometers. The third barrier will be, as for the low-level waste, the dilution and dispersive effect of the vast volume of the ocean. In the case of accident or immediate canister failure only the third barrier may be effective, so it is particularly important to establish its effectiveness.

If leakage does occur, the distribution of isotopes may be influenced by physical processes and by biological processes. In the short-term compared with the long-term the relative importance of these processes may change significantly. The isotopes in high-level waste have half-lives that are exceedingly long relative to the residence times of the waters of the deep oceans (200 years in the Atlantic, > 1000 years in the Pacific). At these long time scales the concentration profiles of elements in the water column are determined by whether their sources and sinks occur deep or shallow, whether they are biologically active or not, and whether they are chemically scavenged by particulates. In the short-term there are a range of biological processes that at first sight could potentially have an important influence on how the isotopes are distributed and dispersed, or could provide transport pathways into organisms that are or could be exploited by Man. This report will describe these processes and will attempt to ascribe some quantitative estimate of their importance to waste disposal problems.

The sources of energy available to the pelagic communities is first discussed because these determine how the communities are structured which in turn will influence how a contaminants will move through the system. The variability at all time/space scale is discussed both in relation to how it may affect fluxes within the communities and how it presents major problems to sampling and hence for monitoring. The vertical structure of the pelagic communities is then described and the various types of vertical movements are discussed both in terms of their importance to the ecosystem and their implications to waste disposal problems. Finally in the summary the main conclusions as to how all these processes may influence the movements of contaminants are brought together.

ENERGY SOURCES FOR OCEANIC ECOSYSTEM

Relatively little is known about how natural or anthropogenic isotopes move within the oceanic ecosystem, so throughout this report it will be assumed that their movements will be determined by levels of biological activity and hence by the patterns of material and energy flow. Clearly this approach will need to be refined as knowledge improves of how naturally occurring analogues of the high level isotopes such as ^{210}Po are transferred through ecosystems.

The major primary input of energy into the oceanic ecosystem is via the photosynthetic utilisation of energy from sunlight to make organic compounds from simple molecules. In coastal seas other sources may be locally important such as riverine and aeolian transport of terrestrial organic material and exports of material from coastal flats. However, it is debatable as to whether there is any significant export of organic production from coastal seas across the shelf break into the deep oceanic realm (e.g. Walsh 1983). Recently it has been sugggested that chemosynthetic processes based on the oxidation of sulphides occuring in the vicinity of hydrothermal vents and some organic rich muds may be of local importance. However, in the vast majority of oceanic regimes the major input of energy occurs within the surface sunlit layers, predominantly by small free-floating phytoplankton. In some tropical seas large floating macrophytes (seaweeds) can form obvious accumulations of standing crop. But even in the Sargasso Sea where these accumulations of floating seaweeds are most obvious, they are thought to contribute only a very small percentage to the total primary production (Howard and Menzies 1969).

There are four taxonomic groups of phytoplankton which make the major contribution to primary production, diatoms, dinoflagellates, μ-flagellates and cyanobacteria (blue-green algae). Other groups such as the silicoflagellates and coccolithophorids sometimes form blooms which may dominate production over limited areas or time periods. Moreover, because of their respective siliceous and calcareous skeletal structures they can make significant contributions to the particulate flux to deep ocean.

A recent development in our understanding of oceanic production is the realisation that in most areas 50% or more of the production is by picoplankton (ie cell <2μm in size); Platt et al. (1983) found that 60% of the production in warm tropical seas passed through 2μm filters. At high latitudes and in upwelling areas turbulence tends to be higher so large cells appear to be better able to keep in suspension and so make a large contribution to the total production.

The rapid attenuation of light even in the clearest oceanic water limits net production to the superficial few tens of metres of the water column. Besides the vertical profile of light intensity, the integrated production level within the sunlit layer (ie the euphotic zone) is influenced by the nutrient supply (mostly nitrogen and phosphorus), the depth of the wind-mixed layer, the growth physiology of the phytoplankton community and the pattern of the animal grazing pressure.

The ratio between production and standing crop is often very high in phytoplankton communities. The build up of large standing crops of phytoplankton (ie blooms) is often limited to seasonal or upwelling events when the growth rate of the community is able to outstrip its reduction by grazing and the sinking out of cells. Both of these processes are influenced by the size of the phytoplankton cells, and result in complex and poorly understood feed-back mechanisms which play an important role in the determination of both the quality and quantity of the phytoplankton stock, and hence the way in which primary production passes into other parts of the ecosystem.

Waste disposal implications

If it is assumed that the movements of any contaminants within the ecosystem are related to the movement of energy and organic material, then the gradient of organic production from the surface layers to the deep-sea would be expected to induce a similar gradient in the contaminants. If the source of the contaminants entering the water column is the seabed, then the flow of organic material will tend to keep them on the seabed. Any contaminants which reach the surface layers by other processes will tend to be removed from the surface to the seabed.

Naturally occurring isotopes will provide direct analogues of how the contaminants may move. One of particular interest is ^{210}Po which is a daughter product of radon emitted from continental sources, hence it has a surface input. It moves rather like a nutrient within the system and its vertical profile with deep water columns reflects its involvement in biological processes. However, it does occur in unexpectedly high concentrations within certain organisms (Cherry and Heyraud 1982) in one exceptional case, high enough for the species to receive doses of α-radiation twice the size considered to be lethal to humans (Cherry, personal communication).

BROAD CLASSIFICATION OF PELAGIC ANIMALS

The classification of animal size groups is based on sampling procedures which are size selective, rather than on functional units within the ecosystem, although there are rough relationships between the size and trophic status of organisms. The initial division is into plankton and nekton. Plankton consists of the smaller organisms which drift passively within oceanic currents and so are assumed not to control their horizontal distribution patterns behaviourally. Nekton are the larger more active organisms which are capable of extensive horizontal movements and so at least have the potential to control their own horizontal distributions. Operationally plankton is sampled by pump, water bottle or small (up to 1-2m^2 nets) with fine mesh (<0.5-1mm) nets, whereas nekton is sampled by medium to large trawls with coarser mesh, large seine nets, or lining techniques.

Plankton is further subdivided into microplankton, mesoplankton and macroplankton. The microplankton is studied by examining water samples collected either in large water bottles or by pumping. It consists of very small fragile organisms which can neither be collected by nets nor very often can they be effectively preserved, including a range of ciliates and tintinids, etc. Their study requires onboard examination of the samples. Mesoplankton are the smallest organisms that can be sampled with fine meshed nets (~35-200μm) and includes smaller crustaceans, larvaceans, larvae etc. whose sizes range up to about 1mm. The macroplankton includes the animals >1mm in length which are effectively sampled with nets with mesh size ranging from 200-500µm.

The plankton is also subdivided into another two categories, the holoplankton which consists of animals that spend their whole life-cycle in the plankton, and the meroplankton which consists of eggs and larvae of either benthic or nektonic adult forms, and so are a temporary component of the total plankton community whose presence may be high seasonal.

Nekton is operationally subdivided into the micronekton which consists of animals reasonably well sampled by the smaller midwater trawls with mesh sizes of 1-10mm and mouth areas of up to 10-25m^2. The larger nektonic animals are too large and/or too active to be taken by such small trawls, and many can only be sampled with non-quantitative techniques such as large (non-opening/closing) commercial trawls, seine netting, lining techniques, or serendipitous methods such as the examination of whale stomach contents.

HORIZONTAL VARIABILITY IN PELAGIC POPULATIONS

All oceanic communities are subject to variability both in time and space. This has been conceptualised visually for zooplankton biomass in the surface layers by Haury et al. (1978) in an attempt to find guidelines for improving the design of sampling programmes and to distinguish achievable goals from the unachievable (Figure 1). It is important to bear in mind that this figure would be quite different for phytoplankton but less so for nekton. These sorts of variation between the responses of phytoplankton and zooplankton is clearly seen in the study by Mackas (1984) on spatial autocorrelation within the plankton community occurring over a continental shelf. Even so in both zooplankton and phytoplankton at scales of 10-100km the along-shore variability had spatial scales three times the length of the offshore variability. There is a linear relationship between the space scales of physical processes, such as diffusion, turbulent mixing and eddy structures and their persistence in time. The variability of the biological processes will have similar space - time relations as the physical processes when the latter are the dominant controlling environmental factors. However, where behavioural or physiological characteristics (e.g. reproductive rates) determine the variability, the biological space/time relationships will depart radically from those of the physical processes. This is clearly seen for example in the influence of diel vertical migration in figure 1.

This variability is not only important to how sampling programmes should be properly designed, but also in indicating where and when biological processes may act synergistically with or independently from physical processes in the movement of materials within the water column. The long half lives of some radioactive isotopes make even the larger space and long time scales of major interest to the assessment of waste disposal.

Large-scale variability (>10 years, >1000km)

In terms of space scales the geographical distribution patterns of both physico-chemical properties and biological characteristics of the oceans carry the inprint of the major oceanographic circulation patterns which are largely driven by atmospheric forcing processes (see Reid et al. 1978). These result in a system of east-west near-surface flows along the equator, flanked by subtropical anticyclonic current gyres which are subdivided by the subtropical convergences and bounded at high latitudes by the polar fronts (figure 2). In the North Atlantic the subtropical gyre is the warmest of all the oceans (probably as a result of the influence of the Mediterranean Outflow Water) and extends to much higher latitudes. Also in the North-east Atlantic there is no clear expression of the subtropical convergence. Instead there is a relatively broad transition zone between the boreal/polar zone where there is extremely strong winter mixing of the surface 400-600m, and the subtropical waters which have a shallow wind-mixed layer overlying a permanent 'seasonal thermocline'. At the polar front the whole stability of the water column is markedly reduced and the seasonal cycle of heating and cooling is reduced at higher latitudes.

These major circulation features (figure 2) create a broad latitudinal zonation pattern in the distribution of both individual species and of plankton communities (see Reid et al. 1978, van der Spoel and Pierrot-Bults 1979). There is also a clear high to low latitude trend from near-surface communities which are species-poor, with relatively large average size, and much larger standing crops, to species-rich communities containing smaller individuals and much higher turn-over rates so that the standing-crops tend to be lower (van Soest 1979). Minor climatic fluctuations cause year-to-year and decade-to-decade variations in the boundary zones (e.g. Colebrook 1978, 1982). Major climatic fluctuations cause substantial shifts particularly in the latitudinal position of the polar front which in the glaciations left a clear signature in the pelagic microfossils occurring in the superficial sediment layers (Cline and Hayes 1976, Shackleton 1982). During the CLIMAP programme comparisons were made of the changes in geographic position of the major oceanographic fronts between the present and 15,000 yr BP at the height of the last major glaciation. In the North Pacific the latitudinal shift in the zones was relatively orderly, but in the North Atlantic the changes were more dramatic. The Polar Front moved south to around 45°N, whereas there was little apparent shift in the transition to sub-tropical conditions (figure 3). Even so, a boreal community was able to enter the Mediterranean and was introduced into the North-West African upwelling zone, where a number of 'glacial-relict' species such as the euphausiid *Meganyctiphanes norvegica* and the myctophid fish *Benthosema glaciale* persist today (Angel 1979).

The study of such climatic variations belongs more to micropalaeontology, than to the study of biological oceanography. However, analogies are drawn between the structure and functioning of the major present-day communities in order to build up a concept of how the oceanic communities were structured in the past. Although the long-lived isotopes have half-lives that are probably long enough to be significant on an evolutionary time-scale so that there could be shifts in the species or subspecies involved, it is most unlikely that major shifts in biological processes have or will occur at such time scales.

Medium scale variability (1 month - 10 years, 50-1000km)

There is now a considerable body of data which has been accumulated about year-to-year variability of oceanic communities through fishery statistics and long-term sampling programmes such as the continuous plankton recorder surveys (e.g. Colebrook 1978, 1982). Although these variations are well documented, there is no adequate understanding of how these variations are generated, other than a general belief that quite minor variations in weather patterns are important. For example in the Porcupine Seabight the spring of 1982 was relatively free of storms and the spring phytoplankton bloom occurred in early mid-April. But in 1983 a series of cyclonic depressions moved through the area, which delayed the onset of the thermal stratification of the near-surface waters and so the spring bloom did not develop until at least late May.

The existence of mesoscale eddies in the ocean has only been recognised for the last couple of decades. This realisation that these features contribute a very large proportion of the dynamic energy in the oceans is even more recent. A major review of these features was initiated by SCOR Working Group 34 (Robinson 1983), in which Angel & Fasham (1983) reviewed the limited amount of biological work which had been conducted on rings and eddies. They concluded that whereas phytoplankton and microzooplankton have life-cycles which are short relative to the time characteristics of the eddies, so that the signature of the eddy is likely to be seen in their distribution patterns, the life-cycles of large zooplankton and nektonic species are too long for there to be a population response to the eddies. However, the nektonic organisms may redistribute themselves behaviourly by horizontal migrations.

Small scale variability (1 day - 1 month, 100m-50km)

These are scales at which phytoplankton distribution patterns tend to be dominated by the physical processes of turbulent mixing (Fasham and Pugh 1976). They include scales at which even relatively weakly swimming nektonic and planktonic species could be capable of modifying their distribution patterns behaviourally, and cover the daily ambits of larger nekton such as whales and larger fish. Many sampling programmes and techniques work close to or within this range of scales, and so are most sensitive to these scales of variability. When multiple serial sampling has been employed to examine horizontal distribution patterns the scales of patchiness have ranged from about 100m (Limacina inflata at 25m in the California Current, Wiebe (1970)), to 208 ± 53m (for 63 species of zooplankton at 550m in the N.E. Atlantic, Fasham, Angel and Roe (1974)). In these studies the parameter that was kept constant was depth, whereas the observation by Haury, Briscoe and Orr (1979) of the occurrence of tidally generated patches in Massachusetts Bay imply that the organisms probably align to some extent along isopycnals (ie σ_t surfaces). This would result in any internal waves generating an observational artefact of patchiness similar to their wave length.

Fine scale variability (<1 day, <100m)

These scales reach down to the ambits of the individual small members of the pelagic communities. At such scales there is no longer the degree of coherence between the biological and physical parameters that occurred at the previous category of scales. At such fine scales ephemeral and unpredictable events become important, for example plumes of excretory products from zooplankters may provide significant if very short-lived 'spikes' of high nutrient concentrations that may be exploited by phytoplankton through a rapid take-up mechanism (McCarthy and Goldman 1979).

The formation of aggregates into marine 'snow' results in photosynthetic activity (Knauer, Hebel and Cipriano 1982) and nutrient levels (Alldredge 1979) being much higher in and around the aggregates than in the surrounding water. Much of this snow is biogenic in origin originating as faecal pellets, detached mucus feeding webs, and discarded larvacean houses (e.g. Taguchi 1982). The role played by these aggregates in sedimentation of organic material in the water column, and chemical scavenging of a great range of substances from the water will be discussed below.

Implication to waste disposal

The high degree of variability in oceanic systems across the whole spectrum of scales in time and space has two major implications to the problems of studying contaminant movement through ecosystems. If the system has noise at a time scale which is comparable in length to the half life of the contaminant, then its pattern of movement within ecosystems will be similarly noisy. The non-linearity of biological systems will also result in noise at one time scale getting transmitted both up and down the spectrum of variability. Modelling such non-linear systems has not proved successful because the models are unstable and are subject to drift. Hence high-precision forecasting by models appears to be an unattainable goal with present techniques. This by no means invalidates the value of 'simple' models so long as their results are considered only to be at best semi-quantitative.

The variability of oceanic ecosystems gives rise to problems of how to study and to monitor the systems. Each sampling technique and programme has its own time/space scales which may not be related to the scales of the process being studied (Angel 1977). It is even possible that the problem is not even accessible to present sampling methodology. This is certainly true for fine scale variability, and could eventually also prove to be the case for long time scale variability; although the geological record does provide some insights, albeit highly selected and distorted, with which to back-check the validity of conclusions. Similarly there are real problems in designing monitoring programmes. There are limits to the precision of any sampling no matter how sophisticated the techniques used, and there will be real problems of distinguishing any signal generated from the noise in the system. The latter problem will become acute if the monitoring is not carried out in the context of a sampling matrix which is adequate in time and space.

VERTICAL ZONATION OF PELAGIC ECOSYSTEMS: ABIOTIC

A number of environmental parameters change with depth which may act either individually or synergistically to induce depth related changes in the water column. The abiotic factors include:-

Light

Seawater is far from being transparent. The attenuation and scattering of light by seawater results in photosynthetic activity being restricted to the surface 150m of the water column in the clearest oceanic water, and much shallower in turbid coastal waters. The degree of attenuation varies with water length, so that there is a progressive shift in the colour of light with depth. Maximum penetration is by blue-green light (wavelength 470-490nm) which is probably detectable by organisms down to depths of 1200m in the clearest oceanic waters (Clarke 1970).

Temperature

In general temperature decreases with depth. In the tropics the surface wind-mixed few tens of metres are uniform in temperature (isothermal). From the base of the wind-mixed layer to a depth of around about 200m is the seasonal thermocline in which the temperature declines very sharply. In the tropics and subtropics the seasonal thermocline is usually a permanent feature, but in temperate latitudes winter cooling results in deep convective mixing which can extend the wind-mixed layer to depths of >500m in the N.E. Atlantic (Pollard and Pu 1984). The seasonal thermocline, or the wind-mixed layer at high latitudes in winter time is underlain by the permanent thermocline which generally extends down to depths of around 1000m. Below the base of the permanent thermocline, temperature declines very slowly with depth. At polar latitudes temperature may be more or less uniform throughout the water column.

Density

Density increases with depth. It is a function of salinity, temperature and hydrostatic pressure, and in the surface layers is predominantly controlled by temperature. Water exchange is thought to occur along isopycnals or potential density (σ_t) surfaces (ie water with temperature and salinity properties which at the surface would have the same density will have the same σ_t properties). Potential density surfaces which occur below the main thermocline in the tropics outcrop at the surface in high latitudes. At polar latitudes the potential density changes very little throughout the water column, so vertical mixing can occur between water at great depths and the surface.

Pressure

Hydrostatic pressure increases steadily with depth by about 1 atmosphere every 10m. Besides its minimal influence on density of the water, it has an important influence on gases both in solution (notably oxygen and carbon dioxide) and as used by organisms for buoyancy. High hydrostatic pressures tend to increase metabolic rates, affect the sol/gel relationships of protoplasm, and change the equilibrium constants of some enzymatic reactions (Macdonald 1975). Consequently, surface dwelling organisms are killed if subjected to pressures equivalent to those occurring at depths of around 2700m (Menzies and George 1972) and vice versa most deep living animals from depths >2500m die if brought up to the surface even if kept cool.

Pressure also plays a role with temperature in determining the dissolution of calcium carbonate. Calcium carbonate in the form of calcite or aragonite is an important compound in skeletal structures in a wide range of midwater organisms. These structures act as attachments for muscles, as protective devices and, as Marszalek (1982) has recently suggested, as a counterweight for fine buoyancy control. Below a critical depth, the carbonate compensation depth, calcium carbonate dissolves. The dissolution depends on the mineralogy of the carbonate, aragonite which occurs in pteropod shells dissolves below about 2500m in the Atlantic, but calcite the main component of foraminiferan shells dissolves below about 4500m (Broecker 1974). The carbonate compensation depth is shallower in the Pacific. Evidence from cores suggests that 60 million years ago, not only was the deep water in the Pacific considerably warmer (~ 15°C) but also the carbonate compensation depth for calcite was at around 1500m (Shackleton 1982)

Nutrients

The general pattern is for nutrients (ie nitrate, phosphate and silicate) to be utilised by the primary producers in the euphotic zone and then either to be rapidly recycled or to sink out into deeper water where remineralisation via microbial degradation occurs. In well mixed water columns, the nutrients are replaced by vertical mixing, but because phytoplankton cells are likely to be mixed below the zone in which there is adequate light, primary production and hence nutrient utilisation tend to be low. When the water is well stratified, there is virtually no vertical mixing and nutrient replenishment occurs slowly by vertical diffusion. However, because phytoplankton is not mixed down, while good supplies of nutrients still remain in the near-surface waters, the cells can grow rapidly. Once the nutrients are exhausted in the wind-mixed layer phytoplankton growth is inhibited, and relies on processes such as nitrogen fixation, vertical diffusion, recycling and upward transport by vertically migrating organisms.

VERTICAL ZONATION OF PELAGIC ECOSYSTEMS: BIOTIC

The vertical attenuation of light restricts the primary source of production, photosynthesis by phytoplankton cells, to the near surface layers of the oceanic water column. All the animal communities in the water column ultimately depend on the amount of production which occurs near the surface. Those that live shallow enough in the water column and are mobile, can migrate up into

the surface layers to feed. However, those that live deep down have to rely directly or indirectly on the rain of detrital particulate material, or need to be able to exploit the dissolved organic substances in the water. The former source is thought to be dominant (eg Vinogradov and Tseitlin 1983, Angel 1984). Within the depth range of vertical migration either the migrants themselves or their faeces, provide a link between the primary source of material above. Otherwise the detrital flux is influenced by a number of factors:-
(a) The size composition of the source population - large organisms produce larger faecal material, and according to Stoke's Law in conditions of laminar flow, larger particles will sink faster than small ones of the same density. Although Stoke's Law cannot be applied to the larger faecal pellets produced by plankton and nekton because they generate turbulent flow as they sink, empirical observations confirm that the larger the pellet the faster it sinks.

(b) _In situ_ water temperature - this influences the rate of microbial degradation of the labile organic material, which may include the matrix which maintains the integrity of the particulate. So the warmer the water the more rapidly recycling occurs and the less material sediments out.

(c) Grazing rate - the interception rate of the detrital rain by the midwater communities will determine how much reaches the communities living deeper down the water column and how much eventually reaches the seabed. Smaller slow sinking particles will be more easily intercepted than larger swiftly falling particles, so the midwater grazing is likely to shift the spectrum of particulates.

(d) Aggregation - the clumping of smaller particles to form larger particles or aggregates is a very important process effecting the sedimentation of organic material in the water column. As they sink aggregates can grow in size by scavenging the smaller particulates they overtake. In addition it is possible (but not yet proved) that bacteria attached to the aggregate may utilise the dissolved organics (DOM) in the surrounding water and so increase the aggregate's mass by growth. However, the bacteria may also cause the disintegration of the aggregates by eroding the structural matrix. The aggregates may also reach a critical size at which they mechanically disintegrate.

(e) The production cycle - the seasonal pulsing of production even in tropical and subtropical seas where the production cycle is relatively smooth is clearly reflected in the fluxes of particulates into deep water (Deuser, Ross and Anderson 1981) and is much more dramatic in temperate seas (Billett et al. 1983).

Vertical profiles of standing crop

The integrated effects of the surface production and detrital fluxes result in an exponential decline in the standing crop of midwater biomass in the deep water column. This was originally described in detail for plankton by Vinogradov (1970) based on collections made using vertically-hauled nets. Wishner (1980a) and Vinogradov and Tseitlin (1983) reviewed the more recent literature. These observations were extended to include micronekton as well as plankton by Angel and Baker (1982) who found that at three geographically widely-spaced stations in the Northeast Atlantic that both plankton and micronekton biomass profiles when expressed in the form $\log_{10}$ (biomass) = $\log_{10}$ a + b had remarkably similar slopes of -3.8 to $-5.3.10^{-4}$ in all but one case (figure 4). These data were remarkably similar to the Russian results which further suggest that in trenches below 4000m the slopes may increase to -6.5 to $-8.5.10^{-4}$ (Vinogradov and Tseitlin 1983).

Close to the seabed conditions change. The sea floor acts as a sediment trap accumulating the whole spectrum of sedimenting particulates. By the time the fine particulates arrive at the abyssal seabed most of the labile organic compounds will have been stripped off them by microbial degradation and will include mainly refractory organics. Larger particles, ranging up from large faecal pellets and aggregates to the corpses of large pelagic animals which sink too rapidly for microbial activity to have time to affect them and are too rare in the water column for them to be exploited by the midwater organisms, probably provide the main source of labile organics. The sediment/water interface is therefore greatly enriched with organic material relative to the overlying water. This enriched source of organic material can become available to the benthopelagic community which inhabits the water a few tens of metres above the sediment. Resuspension by tidal and other currents of fine sediment (eg Pak 1983) and of phytodetritus (Lampitt, personal communication) is known to occur. More dynamic events such as 'benthic storms' which appear to be correlated with pressure effects generated by atmospheric storms (Gardner and

Sullivan 1981), may cause longer-period variations.

Immediately overlying the seabed is a well mixed boundary layer, the nepheloid layer, which is usually observed to occupy the 10-25m layer above the bottom, but can sometimes extends 60-100m up into the water column. The nepheloid layer contains water of greater turbidity as well as of uniform temperate. The influence of the seabed can be observed in chemical profiles to much as 100-1000m up into midwater (eg Spencer et al. 1978), and in regions of rough bottom topography this influence may extend even higher up into the water column (eg Gould, Hendrey and Huppert, 1981). The relative enrichment of the benthic boundary layer results in benthopelagic populations being larger than might be expected from the overlying pelagic populations. Wishner (1980a) observed noticeable increases in standing crops of pelagic organisms occurred within 100m of the sea floor and this effect has been observed again by Angel and Baker (1982) at depths of 4000m off Northwest Africa and by Hargreaves et al. (1983) on the continental slope at depths of 1000-1650m to the south-west of Britain.

On continental shelves and along the shallower regions of continental slopes, the benthic and pelagic ecosystems are intimately coupled and interact. By the time a depth of 4000m is reached the two systems are decoupled, but the depths at which the decoupling occurs is yet to be established. The most likely depth is between 2000-2500m, because these are depths at which high rates of change have been observed in community and possibly trophic structure of both benthic (eg Merrett and Marshall 1981) and pelagic ecosystems (Vinogradov and Tseitlin 1983). The depth at which the decoupling occurs and whether or not this depth varies geographically needs to be established because it may prove to have an important bearing on how easily contaminants move from benthic environments up into the near-surface ecosystems.

Community vertical zonation

The combined influence of both abiotic and biotic environmental parameters produce a clear pattern of zonation down through the water column. Although the vertical ranges of the individual species components seldom exactly match the boundaries of the zones, the interzonal boundaries are narrow strata where the community structure changes rapidly. There are geographical variations in the depth ranges of the zones which leads to some of the variations in the definitions of the zones given by different authors. However, in the Northeast Atlantic these zonation patterns have been extensively studied by members of the IOS Biology Department (eg Angel and Fasham 1975, Fasham and Angel 1975, Fasham and Foxton 1979) and the zonation pattern described here is based on their findings.

Neustonic zone

In the tropics and subtropics, there is a specialised fauna associated with the air/sea interface. Some of the species of the neustonic community have gas-filled floats (eg the Portuguese man-o-war Physalia, and the sailor-by-the-wind Velella), others skate on the surface (ocean strider, Halobates), and others feed along the surface and have eyes adapted for both in air and in water (eg pontellid copepods). The community is predominatly blue in colour, which is presumed to function either as a protection against ultra-violet radiation or as a camouflage against aerial predation. This community is only likely to play an important role in the transfer of nuclides associated with the surface film.

Epipelagic zone

The epipelagic zone extends down through the wind-mixed layer to the base of the seasonal thermocline. It includes the whole of the photic zone and its lower limit lies between 150-200m. In the winter at high latitudes when there is little if any stratification in the surface few hundred metres, the lower boundary of the epipelagic zone may be blurred to such an extent that the surface zonation is no longer recognisable. Venrick (1984) recently showed that no vertical stratification of the phytoplankton community could be seen within a 140m deep wintertime wind-mixed layer, nor was there any horizontal coherence between the samples, so that 'vertical' patches were being generated.

In those seasons and those regions where there is stratification, the daytime epipelagic community typically consists of small-sized, transparent individuals with a large proportion of larval forms. At night the community is swollen by a large influx of migrants from deeper daytime depths. These migrations will be discussed in detail below (see p. 30). The dominant animal feeding mode in the epipelagic zone is that of grazing the phytoplankton, but detritivory and carnivory play important roles. For example, because visual predation is maximum during daylight hours, all animals which are either not camouflaged (for example, by being very small or transparent), or too big for the majority of predators to handle may need to vacate the layers where the light is bright enough for them to be detected.

In shelf seas, the epipelagic zone extends throughout the total water column. Even though shelf seas constitute only around 5% of the total area of ocean they provide about 95% of the world marine fish catch. Even in the deep ocean, a large proportion of the catch of large pelagic fishes is caught within the epipelagic. Hence any routes whereby contaminants may enter the epipelagic communities and their subsequent fate is of direct relevance to the need to estimate dose rates to man. In particular, the exchanges between deep oceanic waters and shelf seas, either physically or via biological pathways is of great importance. In general there is a marked transition in community composition between the open ocean and shelf communities at the shelf break (eg Hopkins et al. 1981) which must reflect a limited exchange between them. On-shelf/off-shelf migrations do occur (eg migrations of eels and salmon) and there are physical mechanisms whereby oceanic water is transported in over continental shelves (eg the warm core eddies observed over the shelf of the eastern seaboard of the USA, see Richardson 1983).

An important feature of epipelagic communities is their heterogeneity in both time and space. As discussed above not only does this heterogeneity create problems in sampling the communities adequately, but it also influences the way in which the epipelagic ecosystem functions.

Mesopelagic zone

The mesopelagic zone corresponds more-or-less to the extent of the permanent thermocline ie from 200-1000m. At or close to the top boundary of the mesopelagic zone the light field becomes totally symmetrical so that it is no longer possible to detect the angle of elevation of the sun. The scattering of the light results in the brightest light coming from directly overhead and there is a symmetrical fall off in light laterally with the dimmest light being back-scattered from directly below (Denton 1970).

Furthermore, the selective attenuation of different wavelengths of light causes a shift in the colour balance towards the blue-green. These changes in the light field open up alternative methods for camouflage at such depths. In the shallow half of the mesopelagic range many fish species have adopted the use of reflective layers which mirror exactly the same intensity and colour of light as the background. These reflective layers are produced by precisely regular layers of pigment platelets which act as interference mirrors. Below around 600-700m the numbers of mirror-sides fishes suddenly decline and they are replaced by dull black or bronze coloured fishes. The sides of these fishes are particularly non-reflective for the blue-green light of the deepest penetrating daylight but also more importantly the colour of most bioluminescence, ie the light produced by the organisms themselves. Many of the larger crustaceans are richly pigmented with red carotenoid pigments which also have maximum absorbance in the blue-green (Herring 1973). The coloration of decapod crustaceans changes from being half red and half transparent, to being totally red at much the same depth as the change in fish morphology occurs.

Throughout the mesopelagic, ventral light organs are used by a wide range of species apparently to break up the organism's silhouette when viewed from directly below. The light organs of the micronekton inhabiting the shallower part of the mesopelagic range (200-600m) by day, tend to be elaborately structured with filters, lenses and reflectors, and the animals possess quite sophisticated systems for comparing the emissions from their ventral light organs with the down-welled light intensity. The species which inhabit the deeper part of the range by day (600-1000m) tend to have much simpler ventral light organs. Moreover these daytime inhabitants of the deep mesopelagic which are diel vertical migrants (see below) tend not to migrate as far as the epipelagic, so it is not surprising that Vinogradov and Tseitlin (1983) reported a sharp decline in the biomass of herbivorous feeding in animals >500m.

Thus on the basis of micronekton morphology, vertical distribution patterns and diel vertical migrations the mesopelagic zone can be subdivided into shallow and deep regions. When considering the plankton and some aspects of the abiotic environmental parameters, the deeper zone can be subdivided further. The lower limit to diel vertical migration by plankton appears to be around 800m (Angel and Baker 1982, Angel in press). 800m also coincides with the maximum expression of the oxygen minimum in many, but not all, oceanic regions.

In a few areas such as the Northwest Indian Ocean and the eastern tropical and subtropical Pacific Ocean, the oxygen minimum reaches low levels and extends over such wide depth ranges (200-1500m in the Panama Basin) so that the majority of species are unable to inhabit these depths (eg Brinton 1979, Longhurst 1976a). These are regions where the high productivity of the surface waters is combined with the source waters for these depths already being depleted in oxygen because of their age (see Swallow 1984 for discussion on NW Indian Ocean). Such low oxygen zones inhibit almost all vertical movements by organisms, but in the northeastern Atlantic the oxygen concentrations never fall low enough to act as such a barrier, except occasionally in the Northwest African upwelling zone.

Angel (1979) examined the population size spectrum in planktonic ostracods off Bermuda and observed that by day the size range and mean size within the population increased across each of these mesopelagic boundaries but remain constant at intermediate depths (see p. 39). This he interpreted as resulting from sudden shifts in predation patterns, but no matter what the cause it indicates a vertical structuring within the pelagic populations which results from environmental restrictions to the vertical movements of the individual organisms.

Bathypelagic zone

The bathypelagic zone extends from about 1000m to about 2700m. Some of the species inhabiting this zone undertake ontogenetic migrations ie their young stages inhabit shallower depths. For example, the ceratioid angler fish have epipelagic larvae which undergo an extensive downward migration at the time of their metamorphosis from the juvenile form to the adult form. At high latitudes seasonal migrations occur between the bathypelagic zone and shallower zones, for example in Calanus finmarchicus the dominant planktonic copepod inhabiting the waters around northern Britain the stage v copepodites migrate down into deep water (to as deep as 2000m in oceanic regions) in autumn (Ostvedt 1955). There they enter a state of diapause, a marine equivalent of hibernation, during which their guts regress and feeding ceases and a large proportion of the body's reserves is in the form of lipids. They remain diapausing at depth until spring. The actual environmental stimulus which induces an organism to break diapause and then to migrate back up towards the surface is unknown (see discussion in Miller et al. 1984).

Generally the inhabitants of the bathypelagic zone are totally dependent on the rain of detrital material sinking into the zone. The main exception seems to be in the centre of some of the oligotrophic gyres where diel migrants extend the ranges of their migrations down into the top few hundred metres of the zone. Food supply is limited and the sources are circumscribed which would be expected to result in a simplified food web structure and a reduction in species richness. However, the diversity in terms of species variety of plankton and micronekton is greater in the shallow bathypelagic than in any of the other depth zones. This probably arises from the much greater stability, both short and long-term, and greater predictability of the environmental conditions in the bathypelagic.

Abyssopelagic zone

The transition between the bathypelagic and the abyssopelagic zone lies at about 2500-2700m. It is most clearly seen in the sharp decline in abundance of fishes. Vinogradov and Tseitlin (1983) state "the overall decrease of biomass occurs mainly as a result of the almost total disappearance of the planktophagous hunters primarily by the disappearance of chaetognaths and small fish, so characteristic for the bathypelagic zone." Angel (1983) considering the vertical distribution of planktonic ostracods at great depths at 42°N 17°W, observed the sudden disappearance of fishes at the transition between the bathypelagic and abyssopelagic zones, and noted that they appeared to be replaced by other predators such as decapods, mysids and medusae (figure 5). However, his sampling did not extend >3900m, whereas Vinogradov and Tseitlin (1983) note that decapods and coelenterates sharply decline in relative abundance below 4000-5000m. There are no clear physico-chemical transitions which can be related to these faunal transitions, except for the carbonate-compensation depth (see p. 17). Angel (1983) postulated that if predation pressure was important in determining community structure, and if availability of food dropped below the critical lower limit at which certain influential carnivores such as fish could not longer subsist, then there would be major shifts in community structure.

The only data that are available for midwater depths >4000m are derived from vertically-hauled plankton samplers and little has been added recently to the information reviewed by Vinogradov (1970). At such depths the fauna is so very sparse that it is difficult to establish with confidence the presence or absence of individual species and hence describe their vertical ranges. Even establishing reliable estimates of community standing crop is a difficult task, partly because the individuals tend to be very fragile and get extruded through the meshes, and partly because contamination with the odd shallow-living animal from shallow horizons during the long periods of time needed to pay down and haul up the sampler, which at shallow depths creates a trivial error, assumes much greater significance.

The fauna inhabiting abyssopelagic zones is poorly known and a considerable amount of taxonomy needs to be done. However, the initial indications are that abyssopelagic species are far more ubiquitous in their zoogeographical distributions than those inhabiting shallower zones (eg Angel 1983). The lower limit of the abyssopelagic is either determined by the influence of the seabed creating a benthic boundary layer or a benthopelagic zone (see below), or at depths >6000m which as described as trench or hadal zones.

Hadal zone

Angel (1982a) reviewed knowledge of trench faunas. Each trench system is a geographically isolated, linear feature. At present the data suggest that there is no evidence of any further vertical zonation other than the steady diminution of standing crop and species richness which results from the extremely low quantities of labile organic material being available at such depths. Only in the King's Trough do depths even approach hadal conditions in the northeastern Atlantic.

Benthopelagic zone

Wishner (1980a) not only demonstrated that there is an increase in biomass which occurs within 100m of the seabed, but also (1980b) that there is a novel fauna associated with it. Hargreaves *et al*. (1983) investigated this fauna over the continental slope to depth of 1650m on the Goban Spur south-west of Britain. They found that the bathypelagic fauna was composed of familiar midwater species, but many of these species were responding to the near presence of the seabed by extending their vertical ranges to greater depths than they normally occur in midwater. At greater depths, however, Boxshall (1983) has described a number of new genera and species of copepod in some samples collected to the south west of the Azores at depths of 3000m. Some samples collected by Discovery in 1977 over a sounding of 4000m to within 10m of the seabed contained 25 species of planktonic ostracod most of which were new to science. This material is still to be worked up, but it indicates that the benthopelagic fauna at abyssal depths is specialised and is apparently restricted to a narrow band of water. If it is indeed restricted then the flow of material from the benthopelagic zone by biological processes will be similarly restricted. The characteristics of this fauna need to be more thoroughly examined.

Implications to waste disposal

The depth zonation indicates that there are limitations to the vertical ranges of individual taxa. Thus there are very few, if any, organisms which can occupy the total water column at any one stage in their life cycle. Consequently no single species is likely to provide a direct link between the deep abyssal seabed and the surface communities. The only possible exception are those benthic species which have pelagic larval stages. However, although at abyssal depths the benthic species tend to produce fewer, larger eggs which have more direct development with an abbreviated planktonic phase, as yet the reproductive and life cycle characteristics of many members of the benthic community at both GME and the Northeast Atlantic low level dumpsite have not been investigated.

Thus any transport by biological processes must be via a trophic chain of species in which there is either predation on deeper living species at extremes of their migrations cycles or specialised detritivory on their excretory products. Even if there existed any clear and obvious examples of such chains, the extremely low standing crop of the abyssopelagic zone will act as a bottle neck to the flux of contaminants.

ZOOGEOGRAPHICAL VARIATIONS IN VERTICAL STRUCTURE

The Northeast Atlantic is the only region for which these variations have been studied. Fasham and Angel (1975) examined the zonation of planktonic ostracods along a section approximately following the 20°W with stations spaced roughly at 10° latitudinal intervals. Analysis of each individual station had consistently provided a vertical zonation as described in the preceeding section. However, when the data from all the stations were analysed statistically another pattern emerged that showed relationships with the distribution of water masses (figure 6). At the northern (high-latitude) end of the section, the zonation pattern was not as clearly defined as at the other stations. Most of the stations were samples in April (although in different years) and this rather blurred pattern in the top 600m is probably the result of the zonation still being influenced by the effects of winter mixing. There was a marked discontinuity between the surface faunas between 40°N and 53°N which coincides with the separation between the permanently and seasonally stratified waters. The station at 18°N appeared to be in a transition zone between the rather simply zoned community at 10°N and the more complex zonation pattern at 30°N. The reasons for this became clearer when the group numbers for each similar sample was plotted on a T/S plot (figure 7). The separation related to the community changes associated with the two main water mass types North Atlantic and South Atlantic Central Water. One rather surprising result was that Mediterranean Water did not appear to generate any clear signal in the ostracod community structure (but see below).

Fasham and Foxton (1979) analysed the decapod crustacean data from the set of samples. There were clear similarities between the zonation patterns (figure 8). They then examined some of the features of the general circulation that they considered might be important in creating faunal boundaries, and described a physical zonation (figure 9) which is clearly reflected in both the ostracod and the decapod community patterns. a) the major horizontal zone between the midwater zones 4 and 6 (see figure 9) and the deeper zones 2, 5 and 7 reflect the division of the ocean into the warm water (tropospheric) and cold water (stratospheric) circulations. Two possible boundaries were the 8°C isotherm (shown as solid line in figure 9) or the oxygen minimum depth (dashed line).

b) The shallower boundary between zones 1 and 3 and the deeper zone 4 is the depth of the maximum gradient in the permanent pycnocline.

c) The boundary between zones 1 and 3 is the equatorial divergence which passes through about 15°N at this latitude.

d) The boundary between zones 3 and 4 and zone 6 is related to the boundary between permanently and seasonally stratified conditions in the surface few hundred metres.

e) The boundary to zone 2 is defined by the limits to the spread of Antarctic Intermediate Water into the North Atlantic.

f) The boundary between zones 5 and 7 is defined by the main axis of spread by Mediterranean Water into the Atlantic.

These simply defined boundaries resulted in surprisingly high percentages for goodness-of-fit, and as our knowledge of both physical circulation and biological distributions emerge so it should be possible to refine the precision of these boundaries. Data for other taxonomic groups are now becoming available and help to confirm these patterns. Moreover more recent sampling by IOS is filling in some of the details particularly in the key region between 40°N and 53°N. What is now clear is that the present low level dumpsite in the Bay of Biscay (centred around 46°N 17°W) is similar to the 53°N station and the GME site will be similar to the 30°N station. A limitation to these studies is that they were restricted to the top 2000m of the water column.

Implications to waste disposal

Both the physical structure and the biological structure of the oceanic ecosystems vary geographically. There is a trend for the complexity and stability of both to increase with decreasing latitude, so that upward mixing is less inhibited towards the poles. The variations in oceanic communities which relate to the large-scale current structure may well result in regional differences in the way trace elements including contaminants get distributed within water columns. There are differences in some of the vertical profiles of trace elements between the different gyral systems, but the differences in biological communities have not yet been invoked to help to explain some of these variations. However, this does mean that it is not possible to extrapolate and model confidently using data from one current system to draw conclusions about another. Such extrapolation should be possible between sites within a system.

Major differences occur in the structure and functioning of the pelagic communities between the GME site and the low-level dumpsite to the west of the

Bay of Biscay. The latter site lies to the north of the lower latitudinal limit of extensive wintertime mixing of the surface few hundred metres. Consequently, the seasonality of processes is much greater than at the GME, so that, especially in winter, there is much greater exchange between the bathypelagic zone and the shallower zones. However, there are also much greater pulses of production and probably organic sedimentation which may serve to transport contaminants from the shallow pelagic zones back on to the seabed.

It is yet to be established whether or not the signature of the current gyral pattern can be similarly detected in the abyssopelagic and benthopelagic zones. The very inadequate information available so far suggests that the global distribution of species may be more ubiquitous at such depths, so it may prove possible to extrapolate for modelling purposes interregionally for these deep-living communities.

TROPHIC STRUCTURE OF PELAGIC COMMUNITIES

The trophic structure of the pelagic communities determines the pattern of flow of organic material within the oceanic ~~ecosystem~~ and hence the way in which contaminants will move (figure 10). Contaminants will be taken up either directly from solution in the ambient water or via food. The flow pattern of the contaminant through the community will vary according to whether the contaminant is either absorbed into the body tissues, or remains unabsorbed within faecal material or is taken up onto external surfaces. The latter processes becomes progressively more important the larger the surface area : volume ratios of the individuals become; it is the major process in picoplankton and bacteria.

It is in the epipelagic zone that the trophic structure is most complex. The major input of energy is through photosynthesis, and photosynthetic rates are determined by the available nutrient levels, the integrated amount of sunlight, and the ability of the phytoplankton cells to remain within the sunlit layers. The sizes of the photosynthetic cells determines how they are cropped by herbivorous animals. The larger cells can be sieved from the water mechanically, and this form of filter-feeding has been extensively studied. The smaller cells of the picoplankton cannot be mechanically sieved from the water (see Purcell 1977) and either have to be fed on by very small organisms (ie microzooplankton) or by entrapment such as by mucus-web feeders (eg some pteropods and larvaceans).

However, recent evidence suggests that an important fraction of the picoplankton photosynthetic activity can be associated with marine snow aggregates (eg Silver and Alldredge 1981, Alldredge and Cox 1982) and hence available for cropping by larger filter-feeders.

There are important cybernetic feed-back loops within the system. The abundance of phytoplankton cells can influence the turbidity of the water and the depth to which enough sunlight penetrates for photosynthesis to occur. Nutrient fluxes are greatly influenced by recycling originating from excretion by the animals and remineralistion by the heterotrophs, as well as vertical mixing. For example it has been postulated that the reason for the high productivity of picoplankton is its ability to exploit the excretory plumes released by zooplankton (eg Goldman 1984). How important a contribution is made by dissolved organic material (DOM) to the epipelagic systems is unknown but modelling suggests that potentially it is an important pathway. The main sinks to the system are the sinking out of detrital material (including living phytoplankton) and the export of material in the guts of vertical migrants. Another major unknown is the importance of the so-called microbial loop which initial attempts at flow analysis (Fasham, personal communication) suggest may be more important than previously expected.

The trophic structure of mesopelagic communities is much less complicated. The major inputs are via the vertically migrating organisms and the rain of detrital material. The limited data available suggest that heterotrophic activity and abundances of microzooplankton are both much lower than in the epipelagic (Sorokin 1981). Only the vertical migrants can be herbivores, otherwise feeding has to be based on either detritivory or carnivory.

In the bathypelagic and abyssopelagic zones the structure is even more simplified. The inputs via migrants are substantially reduced, because in most regions diel migrations do not extend down into the bathypelagic, so only relatively long time scale migrations (ontogenetic and seasonal) provide a transport route. Otherwise the only source of organic material is via the detrital flux.

Implications to waste disposal

Much more is known about the structure of epipelagic communities, but their complexity has so far defied comprehensive modelling. An approach which is proving useful at present is flow analysis (Fasham, personal communication) and, if generalisations can be made about the pattern of movement of contaminants within food chains, it may be a potent tool for studying fluxes of contaminants in the epipelagic.

Less is known about the structure of the deeper-living communities, but being simpler should prove more straightforward to model effectively. The distributions of some naturally occurring radioisotopes belonging to the same decay series but which differ in their biological characteristics eg ^{210}Po and ^{210}Pb, offer some hope of quickly establishing an outline of the trophic structure of these communities which will otherwise depend on extensive detailed studies of gut contents and feeding chronologies.

A fuller understanding of the factors controlling detrital fluxes is a prime need. However, present sampling technologies using sediment traps and in situ filtration may not be effectively collecting the particulates of major interest. At shallow depths (<1000m) migrating animals themselves may carry significant quantities of material down through the water column. Deeper down it may be the rarer, larger, faster-sinking particulates that are not sampled which contribute an important fraction of the flux.

VERTICAL MIGRATIONS

The oceanic environment is highly variable in time and space, but vertical gradients are often dominant. Organisms inhabiting the water column not only have to cope with gradients of chemico-physical properties such as light intensity and quality, temperature, nutrients and hydrostatic pressure, but also of biological properties such as productivity, standing-crops, predation pressure and availability of food. These gradients are influenced on broad-scales by water circulation, heat budgets and seasonality, and on smaller scales by mesoscale features, upwelling and finer-scale mixing processes.

Each individual can be thought of as trying to optimize the demands of four basic drives a) the need to survive, b) the need to feed, c) the need to reproduce and d) the need to use its resources as efficiently as is feasible. The demands of these drives are not necessarily compatible, for example at depths where the supply of food is maximal, danger of predation may also be maximum. The level of risk that is acceptable will vary with its stage in the life cycle, its nutritional state (Huntley and Brooks 1982) and its genetical individuality. Iwasa (1982) has produced a simple model based on game theory which shows how diel vertical migration is one of the options open to plankton to solve the conflicting needs to feed adequately and to survive in an environment in which there are complementary gradients of food availability and visual predation pressures if the latter varies daily. However, there are alternative ploys which if adopted will not result in any advantage accruing from diel vertical migration, such as reducing susceptibility to predators (eg by being transparent or invisible), by reducing need for food and staying deep, or merely accepting the high risk of predation.

The higher frequency and the greater the range of a migration, the more significant it is likely to be in contributing to the flux of material through the water column. The movements will only result in a substantial flux if there are gains and losses of material at the extremes of the migration; for example if predation rates are higher at one extreme, or feeding predominantly occurs at one extreme and the retention time of food in the gut is long relative to the time taken on the migration. There are four main categories of movement which may result in active transport of material through the water column 1) high-frequency movements (these may not strictly be defined as migrations), 2) diel vertical migrations, 3) ontogenetic migrations and 4) seasonal migrations. These movements are considered approximately in order of their descending frequency, and hence their potential importance in contributing to flux of material.

High-frequency vertical movements

In the strict sense the diving of sperm whale to catch deep-living squid and/or fish is not a migration, but it is considered here as a potential transport mechanism. Some marine mammals probably present the notable examples of these types of high-frequency vertical excursions. Their need for constant access to atmospheric oxygen coupled with their need to dive for food, can result in a substantial transportation of material from depth to the surface. Most of the standing crop is concentrated in the epipelagic zone, so it is no surprise that most baleen whales do not dive to very great depths, nor do the smaller toothed whales. However, it is the specialist deep-feeding sperm whales which have the greatest known deep diving capability. Lockyer (1977) records some anecdotal evidence of the deep diving ability of these whales. A bull sperm whale was found entangled in a submarine cable at a depth of 1200m off Peru. Another bull taken by a whaler off Durban had a fresh black shark, normally a benthopelagic scavenger, in its stomach on re-surfacing after a prolinged dive over water 3000m deep, the inference being that the whale had taken the shark on the seabed or at least there could be a direct trophic link. However, Lockyer's (1977) own direct measurements of diving depths using Asdic showed that less than 5% of dives were to depths in excess of 800m. So any flux resulting will be limited for the most part to depths of less than 1000m. Seals also dive for food; the maximum depth to which they have been observed to dive is 800m by a Weddell Seal (Kooyman 1968).

There are no data on whether or not any fully aquatic organisms perform similar high-frequency vertical oscillations, but, in the absence of any obvious advantages to the organism that can be postulated, the probability of them occurring seems very small. However, Roe (1974) and later Pearre (1979) have pointed out that present sampling techniques will only allow the discrimination of synchronised movements within a population, so any such high-frequency movements must lie within the total known depth range of each individual species. Depth ranges of species tend to get broader with increasing depth but, because food availability is so low and the gradients within the deep water column so small, it is unlikely that many bathypelagic or abyssopelagic organisms are able to benefit from such energetically-costly movements.

Diel vertical migration

Synchronised vertical movements by some planktonic organisms with oscillations of 24h periodicity have been known to occur for the last 150 years, but the function of these movements has continued to be the subject of active debate (Angel, in press). The normal pattern of movement is for the organisms to swim up towards the surface at dusk. For those animals that migrate right into the surface layers, maximum concentrations often occur near the surface just after dusk. Then they disperse through the wind-mixed layer, producing an effect often described as 'midnight sinking'. At first light once again they aggregate in the surface again (the predawn rise) before swimming (or possibly just sinking) down to the depths at which they spend the daylight hours.

This generalised pattern shows many variations in pattern, in timing and in phase. One modification is reverse migration, when the members of a species spend daylight hours at shallow depths and night-time deeper within the water column.

Generally diel migrations are related to the light cycle, (see Longhurst 1976b for references); the early hypothesis that organisms follow isolumes, has now been modified to the rate of change in light intensity providing the major environmental stimulus (Ringelberg 1964, Bary 1967, Kampa 1974, Enright 1977a). Roe (1983) has recently shown that the vertical ranges of many species are so broad that they span at least three orders of magnitude of light intensity. He (1984) also showed that in many cases the observed rates of ascent and descent of a variety of species (including copepods, decapods, euphausiids and medusae) were much slower than the rate of 120 mh^{-1} at which the isolumes ascended and descended at dusk and dawn (Tables 1 and 4). Enright (1977b) observed comparable rates of 30-90mh^{-1} in the copepod *Metridia pacifica* ie 3.5-10 body lengths per second. Endogenous rhythms (Harris 1963, Enright and Hamner 1967) have been observed and may play a role in minimising the organisms' daytime responses to very short-term stimuli produced by clouds and solar eclipses (Roger 1974a,b, Alldredge and King 1980, Bright *et al*. 1972). Variations in light intensity at night produced by moonlight will be significant where visual predation is important, and so may be expected to cause adjustments to near-surface vertical distributions (eg Roger 1974b).

Longhurst (1976b) in his review of vertical migration listed the various hypotheses which have been advanced to explain diel vertical migration. These are a) avoidance of visual predation, b) horizontal dispersion and transport, and c) bioenergetic advantages, to which perhaps should be added a fourth, breeding migrations.

The avoidance of visual predation

This was one of the earliest theories put forward to explain diel migration (Russell 1927) which came back into vogue with some of the elegant work on the influence of predation on freshwater communities and on cyclomorphosis

Table 1. Estimated ascent and descent rates in mh^{-1} by seven copepod species observed at 44°N 13°W during four sets of 48h observations in April 1974 (Roe 1984a)

	Upward		Downward	
	Mean	Range	Mean	Range
Gaetanus minor	43.0	(32-57)	41.7	(28-65)
Metridia lucens	81.3	(47-130)	61.9	(36-99)
Pleuromamma robusta	84.3	(58-117)	86.2	(57-108)
Chirundina streetsi	85.8	(63-119)	96.8	(66-148)
Euchirella curticauda	107.5	(71-168)	100.2	(69-148)
Undeuchaeta major	122.2	(86-168)	100.2	(69-148)
Undeuchaeta plumosa	122.2	(86-168)	121.8	(99-143)

(see review by Zaret 1980 and Stich and Lampert 1981). The general correlation between migration cycles and light cycles is consistent with this hypothesis. If it is valid, then shallowest daytime depths at which an organism occurs should relate to where it ceases to present a perceptible visual cue. Visual acuity declines with diminishing light intensity and this should create a depth-size relationship with planktonic communities with shallower living communities tending to be smaller in mean size than deep-living (cf. Angel 1979). This could provide a possible cause for ontogenetic migration in which progressively older and larger stages occur progressively deeper by day. In micronekton the depth zonation should be related to camouflage systems and similarly non-migrants may have their visibility reduced by being small and/or transparent. Another effect might be for herbivores to perform reverse migrations where the primary carnivores vacate the surface layers to avoid predation by secondary carnivores. Any pattern of cyclic feeding or migration by carnivores, may confer an advantage to any of its prey undertaking vertical migration even if the predation is unlikely to be visual (eg as for highly transparent organisms such as salps). These are all phenomena which have been reported in the literature.

The size spectra of the ostracod populations in the vicinity of Bermuda increased during the daytime in a stepwise manner with depth (figure 11); each step corresponding to a change in the classical depth zones (Angel 1979). Each one of these steps coincided with a change in the morphology of the daytime nekton community - for example 300m was the ceiling of the distribution of silvery-sided fishes with well-developed ventral photophores (eg myctophids and hatchetfishes) and at 500m there was the change between decapod species that were half red and half transparent to those which were totally red (cf Foxton 1972). There was an ontogenetic change in daytime depths in some of the ostracod species, eg Conchoecia imbricata (figure 12), whereas at night the depth ranges of the oldest juvenile instar and the adults became similar as a result of vertical migration. At night size spectra of the ostracod populations became similar at all sampling depths from the surface to 700m, which was the depth limit of appreciable migration by the planktonic ostracods (but not of the micronektonic species, IOS unpublished data, Donaldson 1975).

Comparative studies of vertical migrations from broad ranging zoogeographical areas would be useful in showing if shifts in predation patterns result in changes in migratory behaviour. Such shifts might be seasonal with the immigration/emigration of key predators or as a result of the normal seasonal succession. In freshwater it has been shown that *invertebrate* predation tends to be non-visual (eg Kerfoot 1977, Zaret 1980) and tends to favour the development of large herbivores 'fitted' with anti-handling devices, such as long spines, and which do not migrate diurnally. At abyssal depth in the oceans there is a trend towards gigantism in invertebrates (Mauchline 1972), often associated with buoyancy mechanisms requiring a large body water content, and possibly predation patterns also play a role in this phenomenon (Angel 1983).

The predation avoidance theory would argue that in the absence of any other advantages, the top predators would not need to migrate. But their presence might well induce migration by their prey; if the prey were also carnivores their migrations may induce an aberrant migration pattern in its food organisms. An example of the complex interactions that can occur has recently been described from a temperate fjord off Washington on the west coast of America by Ohman, Frost and Cohen (1983). There the main herbivore is a *Pseudocalanus* sp. which in August develops a reverse migration, swimming up by day and down at night. Its main predators, a chaetognath *Sagitta elegans* and a copepod *Euchaeta elongata*, both of which are non-visual feeders, become abundant in August. The secondary carnivores, the planktivorous fish (eg juvenile chum, salmon and sticklebacks), feed visually, and their predation appears to induce the two primary carnivores to perform normal migrations. At this time *Pseudocalanus* adopts a reverse migration which the authors postulated minimises the frequency of encounters with the primary carnivores and so results in improved survival. In the absence of predation, *Pseudocalanus* is non-migratory and remains in the surface layers. Experimental studies show that non-migrating *Pseudocalanus* have a higher rate of reproductive increase than migrants, because any increase in fecundity associated with the cooler temperatures experienced by the migrators at their daytime depths is more than offset by a decline in their survival. In this case Ohman *et al*. (1983) estimated that a 16% reduction in mortality through predation is needed for migration to become a better option.

Perhaps one of the major doubts about the hypothesis that avoidance of visual predation is a major cause of diel migration arises from the seas with a uniform deep thermal structure, such as occurs in the Mediterranean and the Red Sea. The pelagic communities inhabiting these seas do not have the same vertical zonation as other oceanic regions and lack a typical bathypelagic fauna (eg Weikert 1980). The usual explanation is that the shallow entrance sills prevent the immigration of bathypelagic species from outside (eg Furnestin 1979), but this does not explain why an endemic bathypelagic fauna has not evolved, hence temperature structure does seem to play a determining role in vertical zonation. The lack of classical vertical structuring of the communities may result in some of the aberrant vertical migration patterns described from the Mediterranean (eg Huré and Scotto di Carlo 1974).

Horizontal dispersion and migration

In a patchy environment vertical movements exploiting the progressive increase in relative shear with depth may be an effective way of either locating favourable patches or escaping from unfavourable ones. The idea originated from Hardy and Gunther (1935) who were trying to explain why it was rare to find patches of abundant zooplankton coinciding with rich patches of phytoplankton. They argued, based on their experience of toxic red-tides, that dense phytoplankton blooms excluded zooplankton by toxic excretions. Now the general consensus is to reverse the interpretation, ie the migrants are seeking out higher concentrations of phytoplankton.

It would seem likely, but it is still controversial, that many filter-feeding herbivores have feeding thresholds governed by the food concentration at which energy expended on feeding exceeds the metabolic gain. Thus rather than avoiding phytoplankton patches, the zooplankton may use vertical oscillations as a means of making horizontal movement to locate phytoplankton patches. Even in microzooplankton such as Foraminifera and Radiolaria it has been postulated that an important function of the heavy skeleton is to provide these non-motile organisms with a mechanism whereby they can sink rapidly and so perform vertical migrations (Marszalek 1982).

There is evidence that at least some plankton is capable of quite extensive horizontal migrations eg the scyphozoan *Mastigias* (Hamner and Hauri 1981) and krill *Euphausia superba* (Kanda, Takagi and Seki 1982). The complexity of the migration pattern in *Mastigias*, observed in a marine lake in Palau, during which an individual animal may move horizontally as much as a kilometre a day and also undergo a vertical migration down to a shallow chemocline at night, warns us against simplistically assuming that planktonic organisms neither undertake nor are capable of undertaking horizontal migrations. Planktonic animals have rarely been observed making horizontal migrations, but this is possibly because field observations have rarely been designed to look for them. It would be a useful modelling exercise to investigate the relative advantages of horizontal versus vertical migration for locating patches of food of different size and frequency, so an adequate programme of field observations can be designed.

Isaacs, Tont and Wicks (1974) investigated the vertical movement of deep scattering layers (DSL's) and showed that the range of migration tends to be reduced in areas of higher productivity probably because of the greater absorption of light which resulted from the higher standing crop. As the relative shear between the surface layers and deep water increases with depth, this would result statistically in the aggregation of the organisms responsible for the DSL within the zone of elevated production. Further evidence for this sort of effect came out of some recent investigations into the biological processes at a front between Western Atlantic Water (ie typical 18°C Sargasso Sea Water) and Eastern Atlantic Water to the Southwest of the Azores. Observed vertical profiles in the two water masses and in the front showed that the integrated standing crop of micronekton was higher in the front and the range and pattern of vertical migration changed quite substantially. The integrated standing crop of phytoplankton as estimated by chlorophyll a concentrations was scarcely higher in the front than elsewhere and insufficient to make a noticeable difference in the observed light profiles. There was no correlation between the migration ranges and the isotherms so the next factor to consider is the distribution of availability of food.

If seeking food is an important function of vertical migration then variations in the quantity and quality of available food might be expected to modify migratory behaviour. On the basis of the Isaacs et al. (1974) model, as food availability declines so the range of vertical excursions might be expected to increase. However, the only reliable experimental evidence comes from the study by Huntley and Brooks (1982) of Calanus pacificus in a plankton tower during which shortage of food inhibited diel vertical migration in the copepodites and they remained at shallow depths throughout the 24h cycle.

In this case, one interpretation could be that by adopting a non-migratory behaviour and remaining at a shallow depth the population of Calanus was following the option giving the maximum probability of survival within the spectrum of space/time variability of its normal environment. For another species from a different ecosystem, or even another race of the same Calanus species, a totally different response to starvation may occur. This whole question of the influence of nutritional state on migratory behaviour needs investigation in a range of species both experimentally and by field observations.

The exploitation of differential current shears between shallow and deep waters is an important mechanism whereby planktonic organisms can avoid dispersion out of a hydrographic system. The time scales of the physical processes in the system will influence which type of migration is important. Thus in estuaries, diel or totally synchronised migrations between the deep inflow and the shallow outflow maintains organisms within the system (Lance 1960, Grindley 1964, Bosch and Taylor 1973). Within larger scale systems such as the Somali Current gyre, *Calanoides carinatus* has a life-cycle tuned to the physical characteristics of the system which, through a combination of diapause and ontogenetic migrations, results in the rich upwelled waters in the upwelling zone being seeded with vast numbers of the copepod (Smith 1982). In such dynamic regions, the distribution patterns of the organism are often much tighter than would be expected if they were merely passive markers. On an even larger scale, the seasonal migrations of *Calanus finmarchicus* have been postulated as the mechanism whereby the zoogeographical distribution of the species is maintained in the N. Atlantic (Jashnov 1970). Kelly *et al.* (1982) showed a similar tuning between life-cycle and distribution in *Geryon tridens*.

Bioenergetic advantages

McLaren (1963) postulated that by migrating between two temperature regimes migrants would be more efficient in their use of energy, since at lower temperatures metabolism is less demanding of energy so more is available for growth. Furthermore, because at low temperatures fewer large eggs tend to be produced, the offspring of migrants would grow faster and be larger for predators to handle and so demographically on balance would have a better chance of survival than the offspring of non-migrants. Few experimental studies have been conducted to investigate this effect, but in a recent experimental study Orcutt and Porter (1983) have shown that in the freshwater species *Daphnia* an oscillating temperature regime gave no added fitness in terms of net population growth; optimum conditions were provided by a uniformly warm environment. McAllister (1971) and Kerfoot (1970) suggested that there is also an advantage to be gained by grazing being pulsed particularly when the growth cycle of phytoplankton is diel with cell division occurring just before dusk. The phytoplankton cells have the maximum daylight period in which to photosynthesize, and feeding becomes more efficient when the cell concentration increases sharply at about dusk. Enright (1977a), recognizing that this theory as stated required a measure of altruism by the species involved (eg Miller *et al*. 1972, McLaren 1974), developed a model that illustrated that there could be a bioenergetic gain to the individual animal if three assumptions were fulfilled. These were 1) the algal biomass can increase appreciably between dawn and dusk, 2) the metabolic needs of the animals are reduced in cooler deeper water and 3) the grazing rate of the herbivores after a period of non-feeding is initially higher than the steady state but declines quite quickly. He showed that one prediction arising out of the model would be that grazers could gain a substantial advantage in migrating up 2-3h before sunset. Enright and Honegger (1977) reported on a sampling programme designed to investigate the timing of migrations and in three 3-day series of samples obtained a measure of confirmation. Off California in early summer the copepod *Calanus helgolandicus* migrated up after sunset, but in late spring both adults and copepodites arrived 1-2 hours prior to sunset. In mid-spring the adults arrived at sunset but the copepodites arrived early implying an ontogenetic change in the degree of advantage in trading off the greater nutritional gain against increased exposure to predation.

Perhaps one assumption by Enright (1977a) that is suspect is that the metabolic needs of animals are reduced at depth. Teal (1971) showed that increasing hydrostatic pressure can stimulate metabolism and so negate the influence of low temperature, although Belman (1978) showed that increased hydrostatic pressure had no effect on the oxygen consumption of the squid *Histioteuthis heteropsis*. In some regions, such as the N.E. Atlantic at 44°N 13°W, the temperature differential between daytime and night-time depths of mesopelagic migrants moving 300-400m may be less than 2°C (eg Roe 1984b). Childress *et al*. (1980) have shown that the metabolism of vertically migrating mesopelagic fish is very different to the non-migrants either from the epipelagic or from the mesopelagic or bathypelagic. The mesopelagic migrants give higher priority to energy storage rather than growth. As sexual maturity is attained so the growth rate declines, and in the case of the myctophid *Benthosema glaciale* there are indications that a switch from a daily cyclic pattern of feeding by juveniles to continuous feeding in adults may occur (Roe and Badcock 1984). Although in developing his model Enright considered herbivores only, his argument could be just as valid for a carnivore if herbivores with full guts are more nutritious than ones with empty guts. However, observations on the time of migrations rarely support the Enright model (eg Roe 1974, Roe *et al*. 1984 and the subsequent papers), but generally there is a considerable lack of suitable observational data.

The most persuasive argument against the importance the energetic bonus of vertical migration comes from the study by Torres and Childress (1983) on Euphausia pacifica. They showed that in the California Current region, the cost of vertical migration cancels any energetic gain from time spent at lower temperatures. They point out that, because their measurements imply that active swimming is substantially more costly than idling, particularly at higher temperatures in water columns where the temperature gradient is small, more energy is likely to be expended by migrating than by staying in the warmer surface waters. However, where the temperature gradient is sharp, such as in the central Pacific where the temperature differential between the surface and 500m is 16°C, a substantial benefit could ensure. Hence the energy bonus of vertical migration is more likely to be important at low latitudes where the near-surface temperature gradient is much sharper.

Breeding migrations

Successful spawning involves two phases, mating (ie sperm transfer) and egg-laying. In many species the phases are simultaneous with fertilisation occurring as the eggs are spawned. However, in some of the species which store sperm and in all of those which brood their young, the two phases may be widely separated in both time and space. Mating requires the successful location of a mate and for small organisms in a vast three-dimensional environment this must pose quite a problem. A solution might be some form of long-distance communication, for example, by the release of sexual-attractant pheromones, particularly is reinforced by one sex either swarming (eg Hamner and Carleton 1979) or releasing its attractant within a layer through which the other sex oscillates. The reduction of the search from 3-dimensional to 2-dimensional, may be the function of mono-sex swarms at the surface, as observed in the males of the ostracod Conchoecia spinirostris (Moguilevsky and Angel 1975). Female swarms have been reported in some shallow water copepods (Ueda et al. 1983); and mixed sex breeding swarms in the euphausiid Euphausia pacifica (Endo 1984). In another ostracod Halocypria globosa males only occur at deep mesopelagic depths (figure 13). Presumably, the females at some time swim or sink down and either locate or are located by the males (Angel 1979). Sexual dimorphism in both vertical distribution ranges and vertical migration is quite a common feature in a whole range of species (eg Furuhashi 1976, Matsuo and Marumo 1982, Hayward 1981).

Ontogenetic migrations

Many pelagic animals change their vertical ranges quite substantially during the course of their life-cycle, and many benthic organisms have pelagic dispersal stages; such vertical movements are termed ontogenetic migrations. In species which have annual life-cycles, ontogenetic migrations will be indistinguishable from seasonal migrations, but in species with either shorter or longer life-cycles these two types of migration will be clearly distinguishable. Ontogenetic migrations can be accompanied by quite substantial metamorphoses of body shape and colour, particularly in the case of some of the deep mesopelagic or shallow bathypelagic species whose larvae are epipelagic.

In those euphausiid species which spawn directly into the water, the eggs are heavier than water; euphausiids store sperm so mating and egg-laying do not coincide. Euphausiid egg sinking rates of 5-7½mh^{-1} have been observed for *Thysanoessa raschi* and *Meganyctiphanes norvegica* (Mauchline and Fisher 1969). Hatching takes place after several days, and so it has been speculated that the eggs of the Antarctic krill *Euphausia superba* may sink to depths of 1500m prior to hatching (Marr 1962). The newly hatched naupliar larvae are non-feeding and start a developmental ascent (see Roe, James and Thurston 1984, for data on other species). They arrive in the surface layers as they moult from the metanaupliar to the first feeding stage, the calyptopis. As the calyptopes continue to mature they start to develop a diel migratory behaviour. Hence the deep water, where particulate feeders are relatively infrequent, is a refuge for the non-feeding stages. The feeding stages then migrate up into the food-rich surface layers, but as they grow and so become more vulnerable to predation, particularly visual predation they tend to develop a diel migratory habit.

If in the oceans, as in freshwater environments, a large size ensures better survival in the presence of invertebrates predation (non-visual), then rapid growth will improve the chance of larval survival. However, as larval size increases so vulnerability to visual predation will increase, so that the selective advantage of undergoing a diel migration behaviour may progressively develop. Thus the type and pattern of predation will influence not only migration but also the life-history 'strategy' adopted by a species.

Another phase of the life-cycle in crustacean plankton at which vulnerability to predation may be increased is the time of moulting. Once again, there appears to be no information published on whether moulting is accompanied either by a change in vertical distribution or by a modification in diel migration.

Seasonal migrations

In regions where production is markedly pulsed seasonally ie at latitudes >40° and in most upwelling regions, seasonal migrations are a strongly expressed feature of the ecology of the pelagic communities. At lower latitudes, there is little if any seasonal adjustment in vertical distributions even when there are substantial hydrographic changes (eg Cummings 1983). Mackintosh (1937) illustrated clearly just how complex are the variations in the seasonal vertical distributions both of the total community and individual species in the Southern Ocean. His work also emphasised just how important it is to be able to understand the broad hydrographic context of a sampling regime; in his case the relative position of the Antarctic Convergence had a considerable influence on the observed patterns.

Generally species migrate to shallower depths during periods of high production, such as during the spring and autumn blooms at temperate latitudes, and move down deeper when productivity falls back either in mid-summer or mid-winter.

In the North Atlantic the dominant copepod species (eg _Calanus finmarchicus_) do not appear to have life-cycles that are highly tuned to the seasonal cycle, possibly either because the climatic changes in the North Atlantic had a more major effect on the temperate planktonic communities, or because at present there is relatively high climatic variability. In quite dramatic contrast in the Northeast Pacific Miller _et al_. (1984) have demonstrated that the dominant herbivorous copepods, _Neocalanus plumchrus_, _N. cristatus_ and _Eucalanus bungii_ have life-cycles that are so well tuned to the seasonal cycle that they seem able to predict the onset of the spring increase in production. They arrive in the surface layers in time for their grazing pressure to prevent the springtime increase in productivity from building up a large phytoplankton standing crop; consequently there is no spring bloom in the N E Pacific comparable to the bloom in the N E Atlantic. These Pacific copepods are able to break and re-enter diapause, and seem able to maintain the abundances of active stages at a constant level in the surface waters by continually topping up the populations from a pool of deep dwelling diapausing animals.

A similar tuning of life-cycle to the physical processes of water circulation is seen in the copepod Calanoides carinatus a dominant constituent of various upwelling regions such as the Somali Current, Peru and the Gulf of Guinea (Smith 1982, 1984). In the Somali Current, the production cycle switches from very poor oligotrophic conditions during the North-east monsoon, to very rich conditions during the upwelling season of the South-west monsoon. The copepod seems able to maintain itself in very high concentrations within the upwelling centres, despite very high surface currents which are known at times to reach speeds of 7 knots. The only possible mechanism whereby a relatively weakly swimming organism can maintain itself in such concentrations is by constantly re-entering the zone via the recirculating deep water. Presumably during the non-upwelling season, the copepods remain within the deep-water eddy circulation in a state of diapause from where they can quickly re-seed the upwelling zone at the change of monsoon.

As with ontogenetic migration, diel migratory behaviour may be superimposed on a seasonal migration. This was observed in the deep-living mysid Eucopia unguiculata in the Northeast Atlantic by Roe (1984b). For much of the year this mysid occupies depths >800m, but in April 1974 at 44°N 13°W the adults had migrated higher in the water column and were undertaking diel vertical migrations between 600 and 450m.

RANGES OF VERTICAL MIGRATIONS

Simplistically it may be thought that downward migrations may not be energetically costly because it could be achieved by passive sinking eg Rudjakov (1972), although examination of observation data shows that for many species the downward movement occurs faster than their sinking rates (eg Roe 1984a, Table 1). The return upward migration might be expected to be energetically demanding because it has to be achieved either by active swimming or by buoyancy regulation. Vlymen's (1970) calculations, however, suggested that for copepods the effort required to undertake a migration is no more than the normal activity required to stay at one depth, whereas Torres and Childress (1983) concluded that migration in Euphausia pacifica is energetically more expensive than non-migration under most conditions. Intuitively it would seem that the cost of migration will increase relative to its range and consequently the advantages accruing to the migrants will need to increase with increasing range of migration. It is also to be expected that the ranges of migrations will be the minimum required to serve the dominant function of the migration. Thus if the main function of the migration is to minimise visual predation, once the migrant penetrates to depths where it can no longer be seen by its predators, then there is no advantage in it going deeper.

In an early report Waterman *et al*. (1939) described a number of species as undertaking extensive vertical migrations from depths of at least 1600m. However, critical appraisal of the results shows that the variations in abundance that these authors observed were within the factor of 2 which occurs in repeated samples at bathypelagic depths (Angel *et al*. 1982). Wiebe *et al*. (1978) interpreted one of their profiles as showing that *Salpa aspera* performed diel vertical migrations to depths of 2000m. However, although their data were reasonably convincing in showing migrations down to depths of about 800m, but there are alternative interpretations (eg spatial patchiness) of the single profile claimed to demonstrate the deeper migration. Angel *et al*. (1982) carried out a series of repeat tows at a depth of 1000m in the N E Atlantic near 42°N 17°W in order to establish the extent of sampling variability and to see if any of the variability had a 24h periodicity. Of 192 species examined only a single myctophid fish species, *Notoscopelus elongatus*, showed a cyclic variability which was consistent with it performing regular diel vertical migrations from that depth.

Subsequent IOS sampling carried out on either side of an oceanic front to the south-west of the Azores (Gould 1984) in the vicinity of 30°N 30°W, showed that in this more oligotrophic region some decapod crustaceans were migrating up from about 1200m (Domanski, personal communication). Even more striking was the migration of another myctophid fish *Ceratoscopelus warmingi* which moved from daytime depths of 1600m up into the surface 100m at night (Badcock, personal communication).

There are surprisingly few data available which allow meaningful interregional comparison of the ranges, seasonal variations and quantitative influences of diel vertical migration on an ocean-wide basis. In the Northeast Atlantic the maximum ranges of diel migration occur at mid-latitudes in the centres of the oligotrophic gyre (IOS unpublished data). Towards higher latitudes the ranges of diel migration progressively reduce. At polar latitudes in the Arctic diel migrations are either much reduced or absent during the summer when the day length is long or even continuous (Bogorov 1946, Digby 1961, Bamstedt 1984). Data from the Antarctic are lacking in seasonal coverage. Mackintosh (1934) analysed some of the early Discovery material collected mostly during the summer season in the vicinity of South Georgia. He explicitly excluded material collected south of 60°S, and he demonstrated variability in the catches of a wide range of species throughout the 24h cycle which was consistent with these organisms carrying out diel vertical migrations. Baker (1959) gave more extensive descriptions of the vertical distribution of the subantarctic euphausiid *Euphausia tricantha.* This species showed a clear ontogenetic development of vertical migration. The adults and adolescents which were present throughout the year migrated up to occupy the surface 100m at night both in summer and winter.

During Discovery Cruise 100 in the 1979 Antarctic summer, Roe (personal communication) made two sets of observations to study diel vertical migration at 57°34'S 22°58'E and 68°28'S 24°17'E. At the most southerly position close to the edge of the pack ice, the structure of the pelagic communities was uniform throughout the surface 500m and showed no apparent diurnal variations. Hence, if migrations were occurring, there was a total lack of synchronisation. At the more northern station where a totally different set of species occurred, cyclic variation in abundance were observed which were consistent with the species undertaking the normal pattern of diel migration.

At equatorial latitudes where temperature profiles are much sharper, the depth ranges of vertical migrations tend to be reduced in planktonic organisms (Angel and Fasham 1975, Roger 1974b), but not necessarily so for micronektonic species such as decapod crustaceans (eg Fasham and Foxton 1979).

In regions where there are very intense oxygen minima, the strata in which there are low oxygen concentrations, will limit the activities of many, but not all vertical migrants. Baird *et al.* (1973) showed that the fish *Bregmaceros nectobanus* penetrated deeply into the anoxic waters of the Cariaco Trench, but other migrants were restricted to depths above the oxygen-deficient waters. Brinton (1979) studied the euphausiid populations of the eastern tropical Pacific, where he found a small group of strong migrators, which could tolerate the very low oxygen concentrations occurring below the thermocline, including *Nematoscelis gracilis*, *Euphausia diomedeae* and *E. distinguenda*. All the other species avoided the oxygen deficient layers.

VARIATIONS IN VERTICAL MIGRATIONS RELATED TO PHYSICAL VARIABILITY

Despite the vast literature on diel vertical migration, there has been surprisingly little effort made to try and quantify the effects of the migration. Longhurst (1976b) attempted some order of magnitude estimates, and using a plankton standing crop estimate of $25g/m^2$ in the surface 100m he assumed a 10% increase from depths >250m, derived an estimated translocation of 2.5 $tonnes/km^2/d$. Maynard et al. (1975) estimated that in Hawaiian waters where the annual productivity is $50gCm^{-2}$, the micronektonic flux into the surface 400m each night is about $2.2gm^{-2}$ which amounts to 44% of the standing crop in the top 1200m of the water column.

During the summer of 1982 the Discovery occupied five stations all within a relatively small area to the southwest of the Azores which were to either side or within a major oceanic front. This front formed the eastern boundary of the main mass of 18°C Sargasso Sea Water (Gould 1984) and also probably represented a boundary of one of the return flows of the Gulf Stream. The specific composition changes very little across the front (Pugh 1975, Angel 1979, James 1984). Yet the depth of the biomass quartiles for both nekton and plankton based on catches to 1400m showed quite substantial variation relative to the front (Figure 14). Estimating the vertical flux of biomass is difficult because daytime catches, particularly of euphausiids, are lower than night-time catches. In Table 2, the night-time standing crops, which have been estimated by integrating up the observed concentrations of catch displacement volumes over the surface 1200m of the water column, are listed together with the percentage decrease in the daytime estimate. If it is assumed that avoidance is constant with depth and each day and night profile is expressed in terms of the percentage of the total water column standing crop occurring within each depth stratum, the percentage increase in standing crop in the top 200m and 500m can be estimated. Because the degree of avoidance probably varies with depth, these estimates are likely to be excessive, for example, in most profiles integrated standing crops for plankton below 500m were almost identical by day and by night at all stations. The percentage of the standing crop moving up into the surface 200m ranged from 6.2-22.2 for plankton and 9.1-32.0 for nekton; the values for 500m are 5.3-15.3 and 9.8-31.4 respectively. The estimates of the fluxes in Western Atlantic Water were lower by a factor of at least three for plankton, but were comparable for nekton. The nekton flux in the front was higher by around a factor of two. In the eddy, the plankton flux was intermediate between the front and Eastern Atlantic

Table 2. Estimates of standing stock (cc displacement volume/m^2) and fluxes resulting from diel migration within the surface 1200m of the water column at five stations all within 300nm of each other close to the oceanic front south-west of the Azores. WAW = Western Atlantic Water (18°C Water); WAWF is a meander in the front; Front within the 20km frontal zone; EAW = Eastern Atlantic Water; Eddy = in core of EAW eddy in WAW spawned two months earlier. Plankton data in parentheses for the WAWF included a nektonic component removed by sorting from the other station data.

	WAW	WAWF	Front	EAW	Eddy
Integrated standing stock					
Plankton	9.3	(23.8)	24.3	16.3	14.2
% Reduction by day	2	28	35	18	- 7
Nekton	5.4	7.4	14.4	9.1	8.7
% Reduction by day	32½	19½	37½	19	0
Flux per m^2 into the surface 200m at night					
Plankton flux	1.2	(1.5)	3.4	3.0	3.0
% standing crop	12.9	6.3	14.0	18.4	21.1
Nekton flux	0.9	1.6	3.2	1.6	1.2
% standing crop	16.6	21.6	22.2	17.6	13.8
P : N	1 : 0.75	(1 : 1.06)	1 : 0.94	1 : 0.53	1 : 0.40
Flux per m^2 into the surface 500m at night					
Plankton flux	0.7	(1.6)	0	1.7	0.9
% standing crop	7.5	6.7	0	10.4	6.3
Nekton flux	1.0	2.1	3.1	1.8	1.6
% standing crop	18.5	28.4	21.5	19.8	18.4
P : N	1 : 1.43	(1 : 1.33)	1 : 00	1 : 1.06	1 : 1.78

Water, but for the nekton it was lower than both. These figures are open to considerable doubt, but they are offered here as tentative evidence that major variations in migration patterns may well occur in relation to hydrographic features.

It is also worth comparing these estimates in table 2 with those of Longhurst (1976b) and Maynard *et al*. (1975) for the translocation of standing crop during vertical migrations. The Longhurst estimated figure of 2.5 tonnes/km^{2}/d into the top 100m, is surprisingly close to the estimates for the planktonic flux into the top 200m given in table 2 (NB if it is assumed that 1cc displacement volume is equivalent to 1g wet weight, then a flux of 1cc/m^{2}/d is equivalent to 1 tonne/km^{2}/d). However, if the micronekton flux is also taken into account then the Longhurst estimate is low by a factor of 2 for the front and EAW stations. There is also a substantial flux up into the surface 500m but this is predominantly by the micronekton, but this is substantially lower than the Maynard *et al*. (1975) estimates. Their estimate of micronekton standing crop in the top 1200m of 4.94gm^{2} is substantially larger than the range of 0.54-1.44gm^{-2} observed off the Azores. Although their estimated flux of 2.18gm^{-2} micronekton biomass into the top 400m as a result of diel migration did not take into account possible avoidance by day, it is still substantially higher than the range of 0.09-0.36gCm^{-2} (17-28% of the standing stocks) observed off the Azores.

Data for individual groups of micronekton are presented in table 3 (Displacement volume data for the front station are unfortunately not available). The day/night disparity probably resulting from avoidance, is most marked for euphausiids, otherwise the disparity only exceeds 90% for fish and decapods at single stations. The disparities based on numerical abundance are very similar. Wiebe and Boyd (1978) in their study of *Nematoscelis megalops* in a Gulf Stream ring believed that avoidance was not a depth related phenomena in this species, and so the shapes of their profiles were not seriously affected. This conclusion is unlikely to hold true for mixed species populations, but in order to get a first order estimate of the fluxes, the day data for each individual profile have been standardised to give the same total water column biomass as observed at night. In those groups for which avoidance may not be a major source of error, the variability between profiles seems to be up to around 10-11%.

Three groups, decapods, fish and euphausiids provide 35-77% of the diel flux in and out of the surface 200m and 50-110% of the diel flux above 500m.

Table 3. Biomass flux cc DV/m^{-2}) of four of the dominant micronekton groups in the RMT 8 samples at four stations in the central North Atlantic. Day data were standardised to give equivalent total water colum (to 1200m) standing crops as night data.

	WAW	WAWF	EAW	Eddy
<u>into surface 200m</u>				
chaetognaths	-0.02	-0.03	-0.03	-0.01
decapods	0.03	0.22	0.20	0.16
euphausiids	0.16	0.11	0.25	0.24
fish	0.10	0.34	0.67	0.40
<u>into surface 500m</u>				
chaetognaths	-0.08	-0.04	-0.01	-0.14
decapods	0.21	0.52	0.43	0.42
euphausiids	0.19	0.14	0.30	0.28
fish	0.39	0.60	0.93	1.10
$\frac{D \times 100}{N}$ for total biomass estimates				
chaetognaths	111	92	101	92
decapods	108	98	74	97
euphausiids	58	79	101	72
fish	77	94	98	89

(The value greater than 100% at the eddy station is mostly offset by the apparent reverse migration of chaetognaths). These fluxes are subject to considerable variability between both taxonomic groups and different hydrographic regimes. These variations in herbivores and carnivores will have an important influence in grazing and predation pressures, in the flow of material through the pelagic ecosystem, and in the recycling of nutrients within the surface 200m.

IMPLICATIONS OF DIEL MIGRATION

Genetic

David (1961) suggested that one effect of diel vertical migration would be to increase the gene flow through oceanic populations. The differential current shear between shallow and deep layers will result in a greater rate of dispersion in species in which the migrations were not precisely synchronized or in which there were ontogenetic or sexual differences in migratory behaviour. However, in species which are adapted to stay within a current or estuarine system the migration will equally well function as an isolating mechanism; any genetical variants whose behaviour becomes less well tuned to the physical system will tend to be lost from the system.

Patterns of grazing and predation

Roe (1984b) and Roe and Badcock (1984) have summarised part of a vast array of feeding data and show how the chronology of feeding varies considerably between different migrants and non-migrants. Even within an individual species such as the myctophid fish, feeding chronology changes during development. The diets of species that feed continuously during their migration cycle changes, partly because of changes in prey availability and partly because of selectivity changes. Roe's (1984b) data for the decapod *Systellaspis debilis* are shown in figure 15 and illustrate the changes in diet that occur between day when the animal was abundant at 450m and night when it was abundant at 100m. Roe (1984b) was also able to show that the two species of *Acanthephyra* never directly competed in time or space. Thus migration probably leads towards greater resource partioning in many cases. It would be interesting to contrast the migratory behaviour and feeding patterns of similar pairs of species between regions where the pairs either co-occur or do not in order to look for evidence of character displacement. Character displacement (eg Angel 1982b) is evidence of interspecific competition between closely related species, and may be limited seasonally or to certain parts of the life-cycle.

The way in which variations in predation pressure, and possibly competition, may feedback into the function and structure of pelagic ecosystems is illustrated by the work of Ohman, Frost and Cohen (1983) discussed above. However, considerably more data are required on the feeding chronology and physiology together with selectivity in diet of midwater organisms. The same limitation is evident in the way in which vertical migration influences the flow of energy and material through pelagic ecosystems.

For migrants to transport substantial quantities of radioisotopes up through the water column, they need to feed extensively by day while at the deeper end of their migration ranges. While Roe and his colleagues (1984) have shown that some migrants do apparently feed continuously, many (eg the myctophid fish Benthosema glaciale) feed mostly at night and very little if at all by day. Thus if this pattern of feeding chronology is confirmed more broadly then diel vertical migration will tend to assist with the removal of isotopes from the near surface layers rather than transport them upwards.

Energy flow through ecosystems

Vinogradov (1970) postulated the migration ladder hypothesis to explain how sufficient organic material reaches deep-living communities. Since then extensive sediment trap data have suggested that 10% of surface production sinks below 400m and 1-3% reaches the seabed at depths of 5000m (eg Honjo, Manganini and Cole, 1982). However, Angel (1984) has argued that the sediment traps are 1) unlikely to catch the large, rarer faecal material produced by nektonic organisms, 2) they will totally miss all the material which moves down within the guts of migrants. Actual migration rates of micronekton (see Table 4) are as fast or faster than the sinking rates of large faecal pellets - some salp faecal pellets sink at 1000-2000m/day which is equivalent to 40-80m/h (see Angel 1984). The deeper a pellet is released the lower is its likelihood of either being intercepted in midwater because of the progressive decline in the standing crop of deep-living detritivores with depth (eg Angel and Baker 1982), or of being substantially degraded by micro-organisms because of the cold water temperatures. So, if the gut-retention times of extensive migrants is such that they void their guts at daytime depths before beginning their dusk ascent (which

Table 4. Estimates of estimates of micronekton migration rates (mh^{-1}) mostly mean population estimates (from 1. Roe 1984a, Roe, James and Thurston 1984; 3. Roe and Badcock 1984; 4. Torres and Childress 1983).

<table>
<tr><th></th><th></th><th>Ascent</th><th>Descent</th></tr>
<tr><td><u>Systellaspis debilis</u>[1]</td><td></td><td></td><td></td></tr>
<tr><td></td><td>adults</td><td>63.8</td><td>68.4</td></tr>
<tr><td></td><td>juveniles</td><td>55.4</td><td>43.8</td></tr>
<tr><td><u>Gennadas elegans</u>[1]</td><td></td><td>41.4</td><td>33.6</td></tr>
<tr><td><u>Atolla vanhoeffeni</u>[2]</td><td></td><td>50</td><td>60</td></tr>
<tr><td><u>Euphausia krohni</u>[2]</td><td></td><td colspan="2">76</td></tr>
<tr><td><u>Benthosema glaciale</u>[3]</td><td></td><td>~ 100</td><td>~ 100</td></tr>
<tr><td>DSL in San Diego Trough[4]
(probably <u>E. pacifica</u>)</td><td></td><td>60-270</td><td></td></tr>
<tr><td><u>E. pacifica</u> experimental[4]
maximum</td><td></td><td colspan="2">350</td></tr>
</table>

could reduce the organisms density and so make the ascent less expensive in energy), the migrants could make a substantial contribution to the flow of material into deep water. Hence the flow of labile organic material could be much faster than is generally believed at present, and much more directly linked to surface productivity in regions where, and at times of year when, migration ranges are extensive.

To illustrate the approximate level of the fluxes, the daily migration of 1gm fish per m^2 in and out of the surface 500m at the eddy station can be used to estimate the faecal flux. If it is assumed that the daily ration is 10% of the body weight, the assimilation efficiency is 50%, the carbon content is 5% and all faeces are voided at depth, then the fish alone will transport 2.5mg C per day down out of the surface 500m. This represents 0.4% of an annual production of 250g C $m^{-2}y^{-1}$ and, as faeces at least some is likely to sink at rates of $1000md^{-1}$. Most would be expected to reach the seabed and would provide an additional input equivalent to 15-40% of the flux measured by sediment traps; a further 10-25% may originate from euphausiid and decapod faeces. If these calculations are of the right order of magnitude, then vertical migration may have a significant influence on the sedimentation of organic material to the deep-living communities and on the chemical profiles of elements and compounds whose distributions are influenced by the organics. However, these estimates are sensitive to variations in assimilation efficiency, so if an assimilation rate of 95% is assumed, as might occur for nitrogen, migrants will contribute an order of magnitude less to the downward transport. Hence shifts in C : N ratios may provide useful insights into some of these processes. Evidence for the rapid transportation down deep water columns is beginning to emerge (eg Walsh 1983, Billett et al. 1983), but it is not always easy to reconcile some of the carbon isotope data, particularly from the N. Pacific, with such rapid transport (eg Pearcy and Stuiver 1983).

Implications to waste disposal

Diel vertical migration involves the highest frequency, global mass movement of organisms known, and hence provides the mechanism with the greatest potential for shifting contaminants within the water column. However, it is all restricted to the surface 2000m and most to the surface 1000m. Because of the general decline in standing crop with depth, even if feeding was continuous there would be greater transportation potential down rather than up. However, studies on feeding chronologies show that in some species little if any food is taken at depth and all feeding occurs at night when the animals are at their shallowest depths. In these circumstances if the gut retention times are long relative to the time taken for the downward migration, then substantial downward transport of material could be occurring. However, if the contaminants occur in solution in the deepwater rather than absorbed or bonded onto particulates, then the migrations could result in upward transportation.

Implications of ontogenetic and seasonal migrations

There have been few attempts to try and estimate quantitatively the movement of biomass involved in these migrations, although they will clearly result in modifications of the flow of material through the food-web. This is probably partly because there is a lack of seasonal coverage in most oceanic areas, but also because the feeding relationships are not clear, for example diapausing organisms overwintering at depth do not feed.

Hargreaves _et al_. (1983) in their analysis of biological processes occurring close to the seabed in a continental slope region discussed the potential flux which might originate from the seasonal migrations of the abundant medusa _Aglantha digitale_. Williams and Conway (1981) had described how, at 59°N, 19°W in the Northeast Atlantic, large numbers of mature specimens arrive in the surface 100m from May onwards, reaching peak abundances in June. This is presumably a breeding migration because simultaneously abundant numbers of the smallest juvenile forms appear suddenly in the near-surface layers. These larval forms continue to build up in abundance through June and into mid-July. In mid-July the vertical range of the smaller forms began to extend down to the lowest limits of sampling at 500m. Hargreaves _et al_. (1983) observed high concentrations of this species just above the seabed at slope depths of at least 1120m in late July, and in a mid-oceanic area Angel _et al_. (1982) observed this species in abundance at 1000m in April at 42°N 17°W, and yet Roe, James and Thurston (1984) found it to be abundant at 100m at 44°N 13°W again in April.

Williams and Conway (1981) reported that the maximum densities of the mature medusae were about 1 per $10m^3$ in the top wind-mixed 100m of the water column. The maximum weight of the mature forms was 4mg (= 2% of wet weight), so the total upward flux from depths of ~ 1000m would have been around $40mg/m^2$. The flux back down through the water column of juveniles in late summer will probably be be greater, because losses to the standing crop through mortality at depths are likely to exceed any gains resulting from growth. Miller et al. (1984) reported mortality rates of around 2-3% per day in the overwintering diapausing stock of Neocalanus plumchrus in the Northeast Pacific, so that the population concentration fell by nearly two orders of magnitude during the winter period. If such results are typical, then the upward flux resulting from seasonal migration is likely to be substantially smaller than the early downward flux. When this is considered on a total community basis, then the total annual seasonal migration can be guessed to be equivalent to about half the deep-mesopelagic standing crop observed in the early spring prior to the spring bloom. Angel and Baker (1982) observed the total planktonic standing crop between 900-2000m in the Porcupine Seabight region to be $16gm^{-2}$, so the upward seasonal migration is possibly in the order of $5-10gm^{-2}$.

A similar very rough estimate can be made of the flux resulting from reproduction by deep mesopelagic and bathypelagic organisms, using inferences derived from Childress and Price's (1978) observations on Gnathophausia ingens, a large mysid which is not necessarily typical of other mesopelagic species but happens to be the only species for which there are good data. This mysid has a 7-year life-cycle. It produces a single clutch of eggs, which it broods. Up until its final instar the mysid grows exponentially approximately doubling its body weight, but after the final pre-reproductive moult it shows little or no increase in body weight. Hence its final reproductive investment is probably equal to its final body weight. If it is assumed that 20% of the species inhabiting the 1000-2000m zone have ontogenetic migrations into the surface 1000m of the water column and that 10% of these are sexually mature at any one time, then the ontogenetic flux will be about 2% of the standing crop. Angel and Baker's (1982) combined plankton and micronekton data for this depth stratum at two N.E. Atlantic stations was $18-27gm^{-2}$, and on this figure the ontogenetic flux will be of the order of $0.5gm^{-2}$. Scanty though the data are for this 'estimate', the resultant figure is unlikely to be more than an order of magnitude in error.

SUMMARY

The GESAMP Report (1983), on a model for the dispersion of pollutants in the ocean, concluded that there was nothing in our present state of knowledge of oceanic pelagic ecosystems to suggest that any biological processes will make a contribution that approaches within two to three orders of magnitude to within the dispersion by physical processes. There is nothing contained within this report that casts any doubt on the validity of this conclusion; however, it must be stressed that despite the considerable growth in our knowledge and understanding during the course of the last five years, it is still impossible to have the necessary degree of confidence in this conclusion.

There are some generalistions that are consistent across a wide spectrum of oceanographic studies which are relevant to the problem of whether or not biological processes will result in upward fluxes of contaminants which will be large enough to cause concern.

The main energy input into oceanic ecosystems is in the surface photosynthetic zone. The deeper a community lives, the more remote it will be from its primary source of energy and material, and so the more the supply will be attenuated. If the standing crop remains constant, its turnover in the absence of substantial import or export of material will equal the supply. If there is a substantial amount of export of material, in this case by recycling it back up to the surface layers, it must be much less than the supply because no biological system is 100% efficient in converting food into growth.

Any flux resulting from processes occurring within a community will be proportional to the production within the community. Although measures of standing crop give no real estimate of production unless turn-over rates are known, the very small standing crops observed in deep pelagic communities, combined with the very few data available which suggest that their turn-over rates are also very low, imply that production in the deep-living communities is similarly very low.

The dominant fluxes of biological material are down the biomass gradient, ie from the euphotic zone to the seabed, althought there is active recycling within the surface 1000m as a result of migrations. Below 2000m there is no evidence of migrations and vertical recycling is unlikely to be measurable. The

The best estimates available suggest that only 1-3% of surface production sediments our onto the abyssal sea floor and of that only a small percentage get incorporated into the sedimen (Muller and Suess 1979). Known benthic standing crop levels together with what few data are available on benthic turn-over rates suggest that most of the input is either used up by the metabolism of the benthic community or incorporated into the sediments.

Chemical scavenging by the rain of particulate organic and inorganic material is known to transfer naturally occurring radioistopes with atmospheric inputs quite rapidly down to the seabed. It will be just as effective at scavenging and returning any contaminants which escape up into the water column back on to the seabed.

The limited vertical range of both planktonic and micronektonic species together with the pattern of vertical zonation results in there being no direct biological transportation route from bed to surface within the oceanic water column. Any transport will have to occur through a number of links in a food chain. Within the abyssopelagic zone the paucity of standing crop makes it most unlikely that there is any important upward flux. Even in the few species that do have relatively extensive vertical ranges such as _Eurythenes gryllus_ the scavenging amphipod it is thought that individuals rarely if ever traverse the whole vertical range during their life times (Ingram and Hessler 1983). However, there are a number of records of these amphipods being spewed up by sea birds.

Within the surface 2000m vertical migrations could well provide transportation routes up into the surface strata of the water column. The greater the frequency of the migrations and the greater the mass of organisms migrating, the greater is the potential for transportation. The highest frequency migrations are probably the feeding dives of some of the larger marine mammals, notably the sperm whales. The decline in whale stocks and the moratorium on whaling in many regions reduces this potential route to man. Diel vertical migration provides the next most frequent vertical movements, and probably results in the greatest flux of material in and out of the surface layers. At present none of these migrants are directly exploited for human consumption but they are food for commercially exploited stocks of large pelagic fishes (mostly scombiform fish _Thunnus_ spp. _Euthynnus_ sp. _Xiphias gladius_, and _Auxis_ spp.) and potentially important stocks of cephalopods. Ontogenetic and seasonal migrations can cover much greater vertical ranges but in terms of the annual flux of material the probability is that these migrations do not create an important transfer route.

Because of the vertical restriction of these migrations to the surface 2000m, they will only become important where other processes move the contaminants up into this zone. This is more likely to occur in two sorts of area, at high latitudes and along continental slopes. Physical mixing will be most intense horizontally moving along surfaces of constant density (isopycnals). These shallow towards high latitudes and may bring contaminated water within the ranges of the migrations. Along continental slopes physical processes tend to be more dynamic and vertical ranges of pelagic organisms tend to extend down into deeper water. In the Northeast Atlantic deep winter convective mixing is restricted to the upper 600-700m, and the localised upwelling along the shelf break is limited to even shallower depths. The persistence of Mediterranean Outflow Water alongs its extension well north to the west of the UK, illustrates how horizontal spread is far more active than vertical spread. However, in the Porcupine Seabight region there is apparently extensive mixing of the Mediterranean Water (unpublished data Discovery Cruise 105), so in localised areas vertical mixing may prove to be more extensive because of such topographic features. The importance of continental slopes is their close proximity to the shelf seas which are heavily fished commercially.

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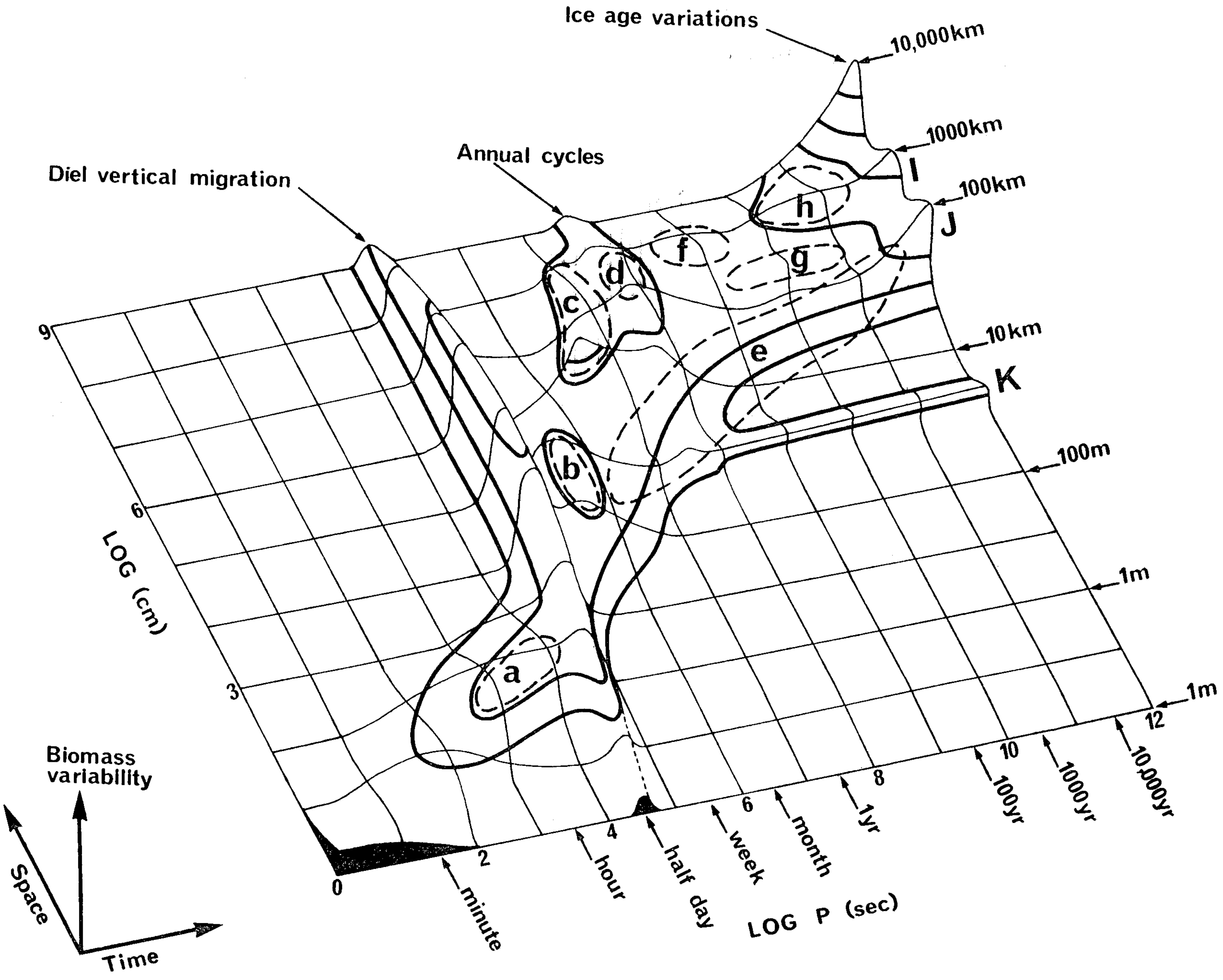
FIGURES

Figure 1. A Stommel diagram giving a visual impression of the possible relationship between variability of zooplankton biomass in time and space showing maxima associated with a. 'micro' patches; b. swarms; c, upwelling events; d. mesoscale eddies and rings; e. island effects; f. El Nino events; g. small scale oceanic basins; h, biogeographical provinces; i. length of current and oceanic fronts; j. width of currents; k. width of oceanic fronts. (After Haury, McGowan and Wiebe, 1978).


Ice age variations
10,000km
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Annual cycles
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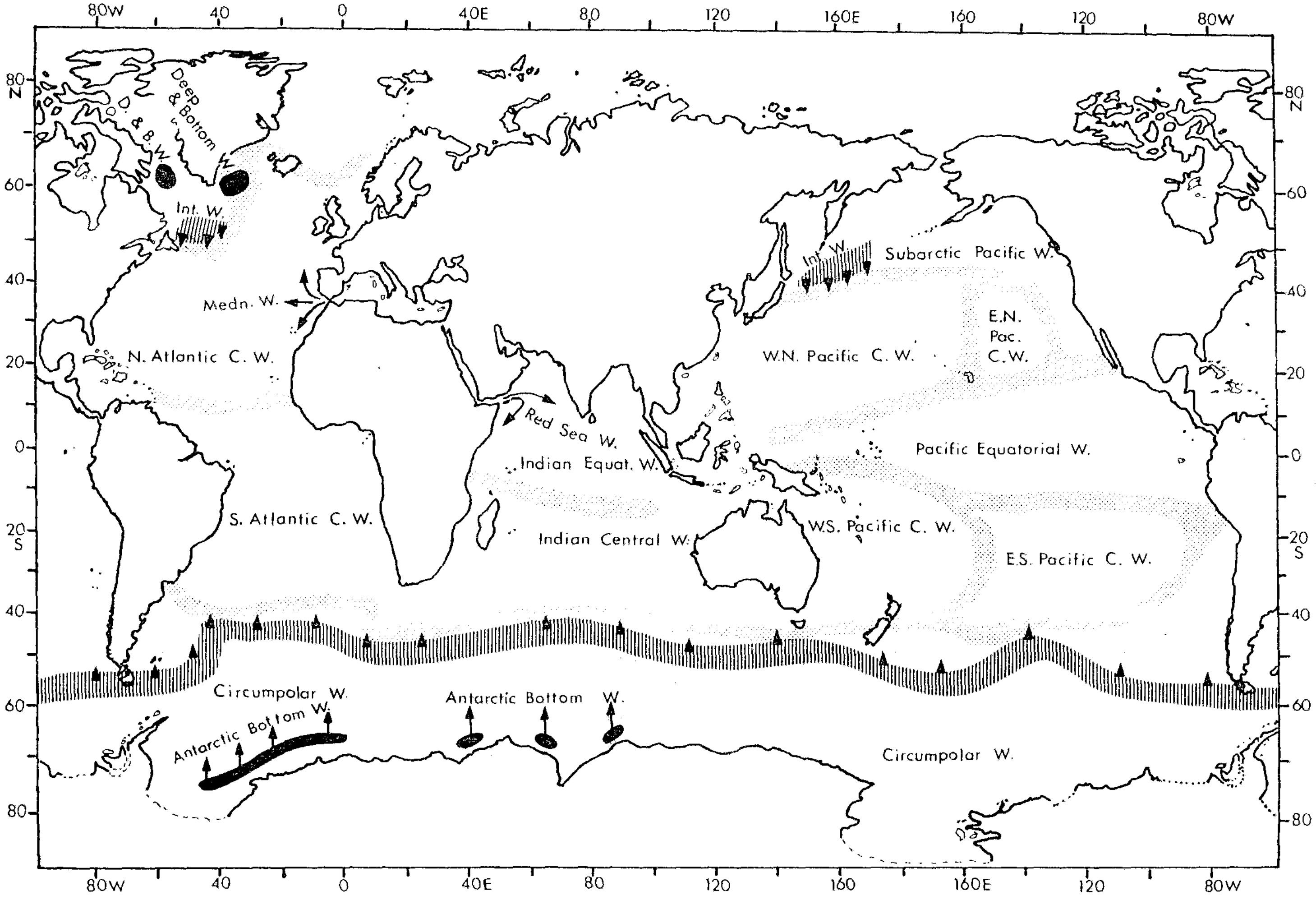


Fig. 2A Geographical distribution of the major water masses of the World's oceans showing the regions where bottom water masses and intermediate waters are formed.

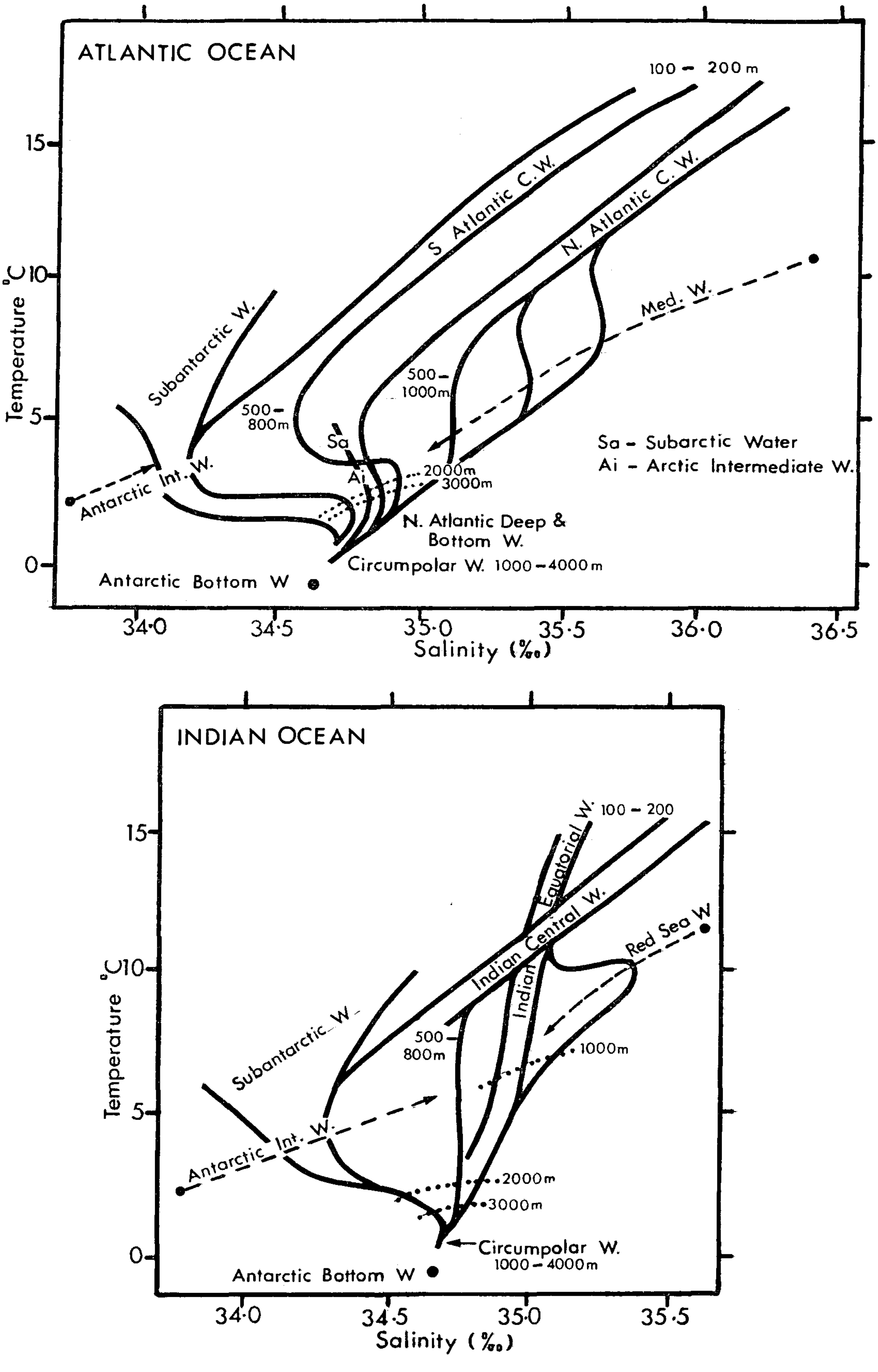


Figure 2B. T S relationships of the main water masses in the Atlantic and Indian Oceans.

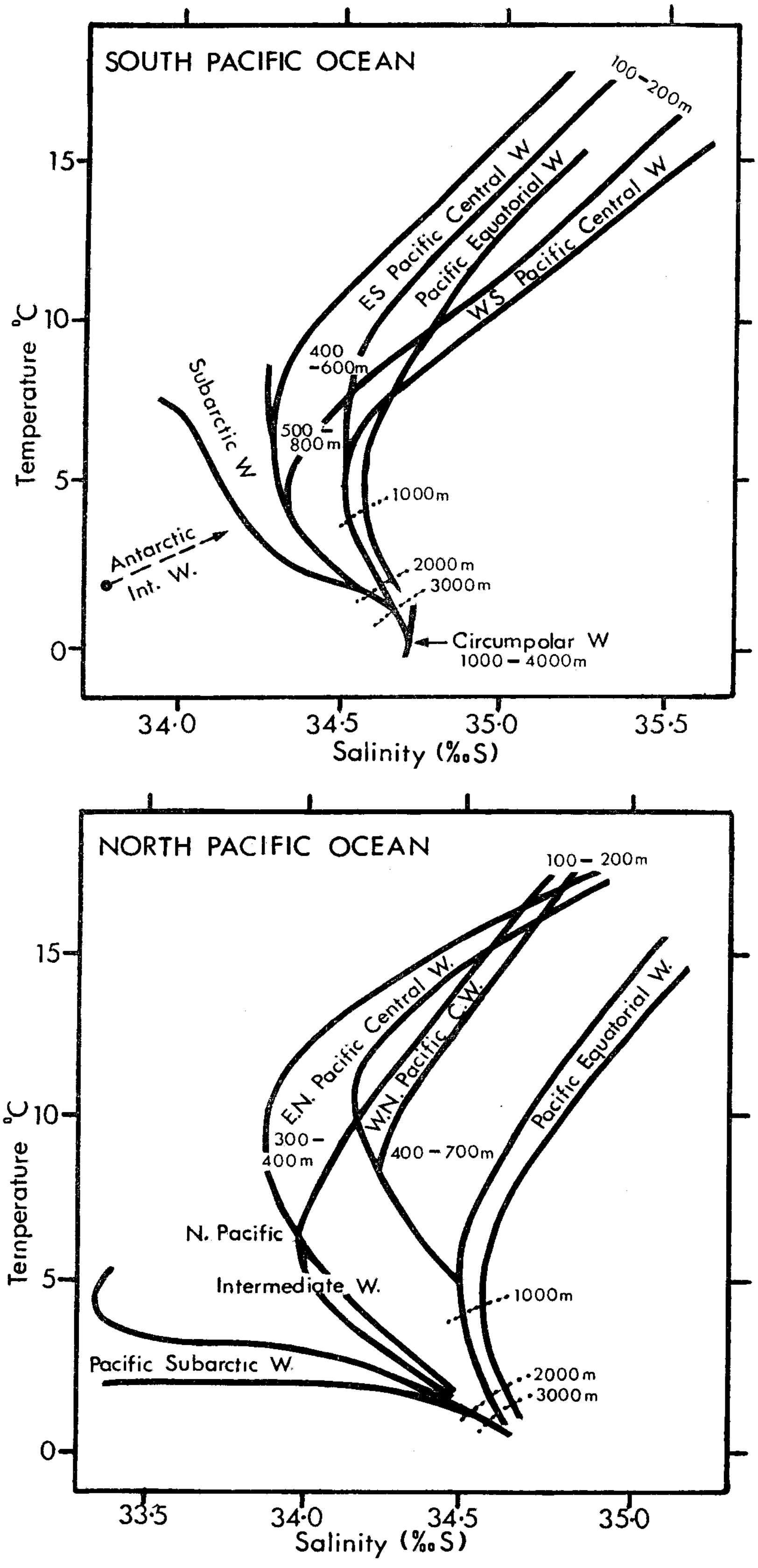


Figure 2C. T S relationships of the main water masses in the North and South Pacific (all modified from van der Spoel and Pierrot-Bults 1979).

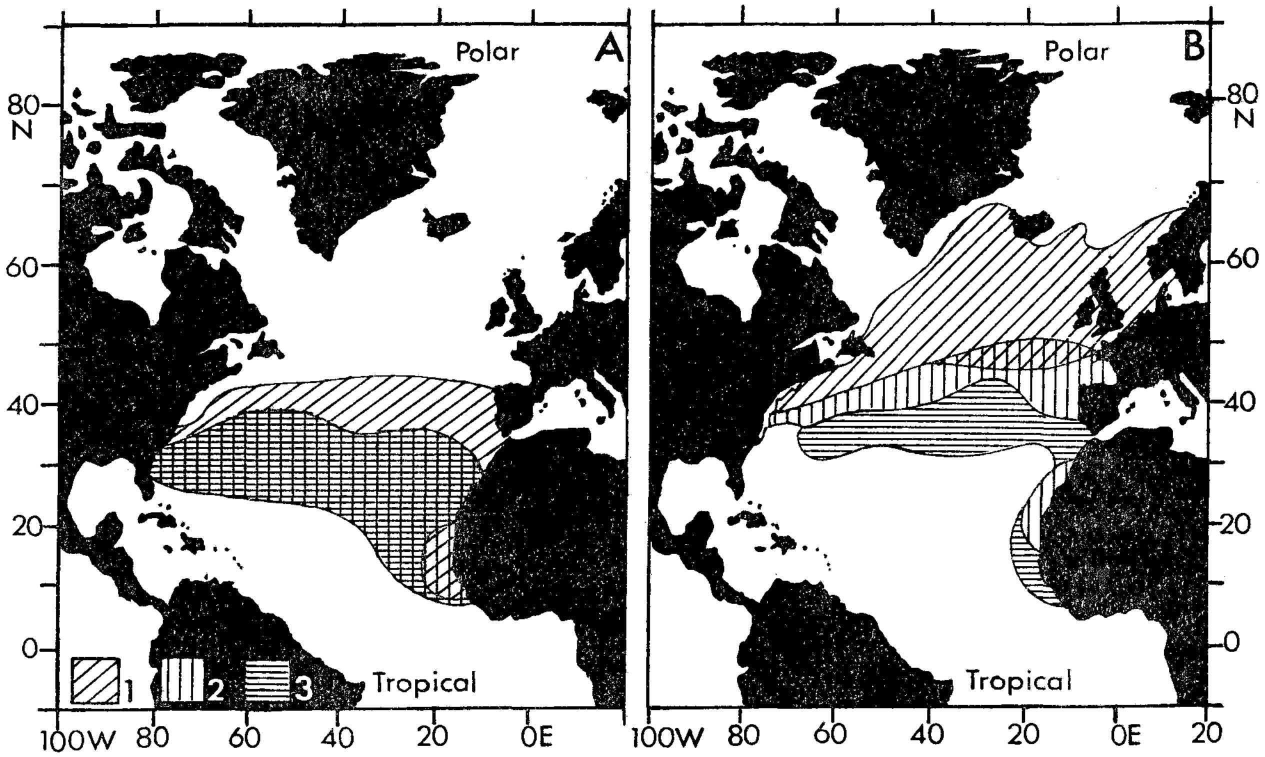


Figure 3. Distribution of the main zoogeographic associations of species in the North Atlantic based on the results of the CLIMAP experiment. A: 18000 years BP and B: at present. 1 = subpolar, 2 = transitional and 3 = subtropical communities (after Cline and Hayes, 1976).

3

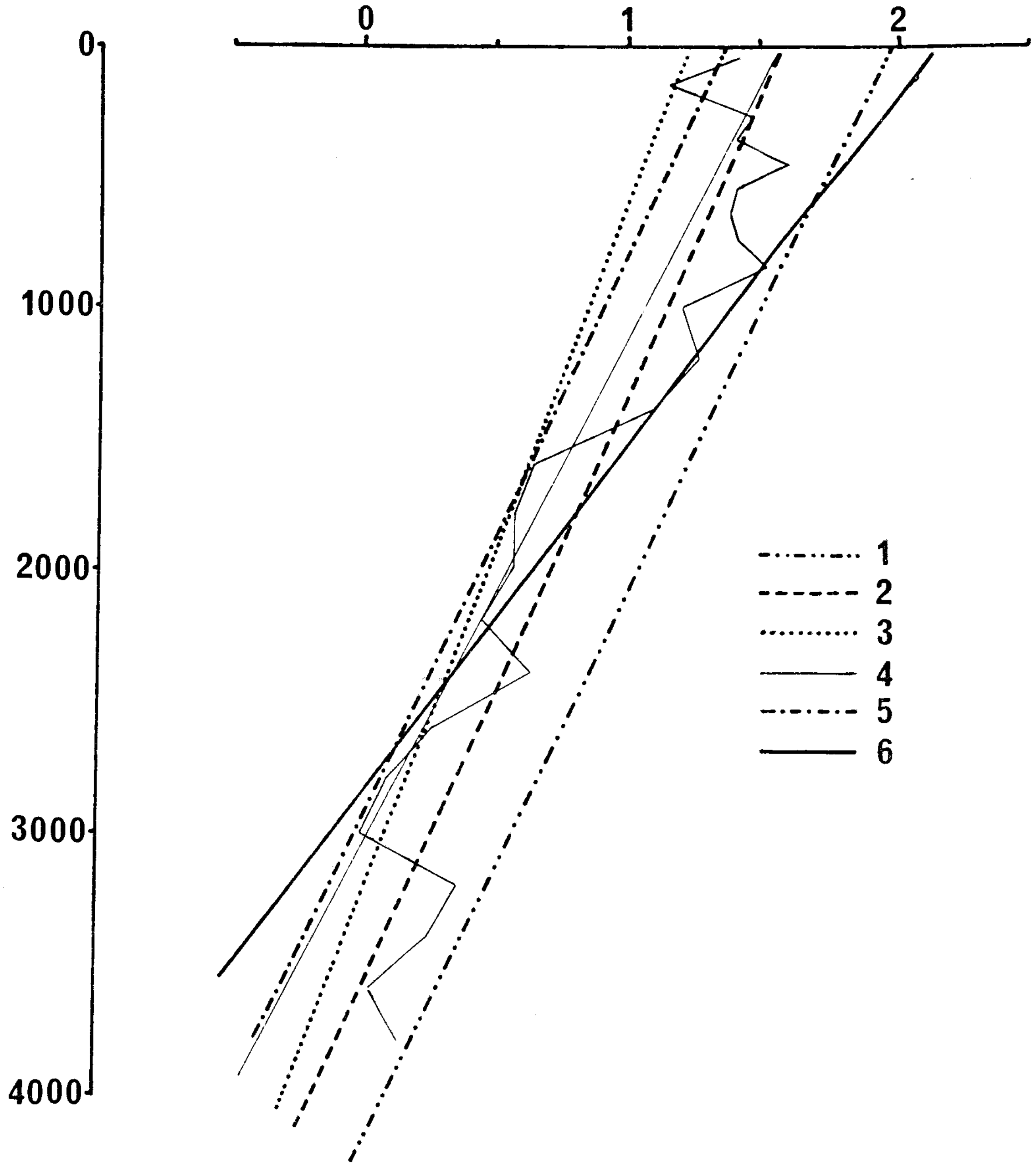


Figure 4. Regression lines of the vertical profiles of log (biomass) against log (depth m) for plankton and micronekton at three stations in the Northeast Atlantic:- 1) for micronekton at 20°N 21°W; 2) for plankton at 42°N 17°W; 3) for micronekton at 20°N 21°W; 4) for plankton at 49°40'N 17°W; 6) for plankton in the N E Atlantic according to Wishner (1980a). Superimposed is the raw data profile for micronekton at 42°N 17°W (after Angel and Baker, 1982).

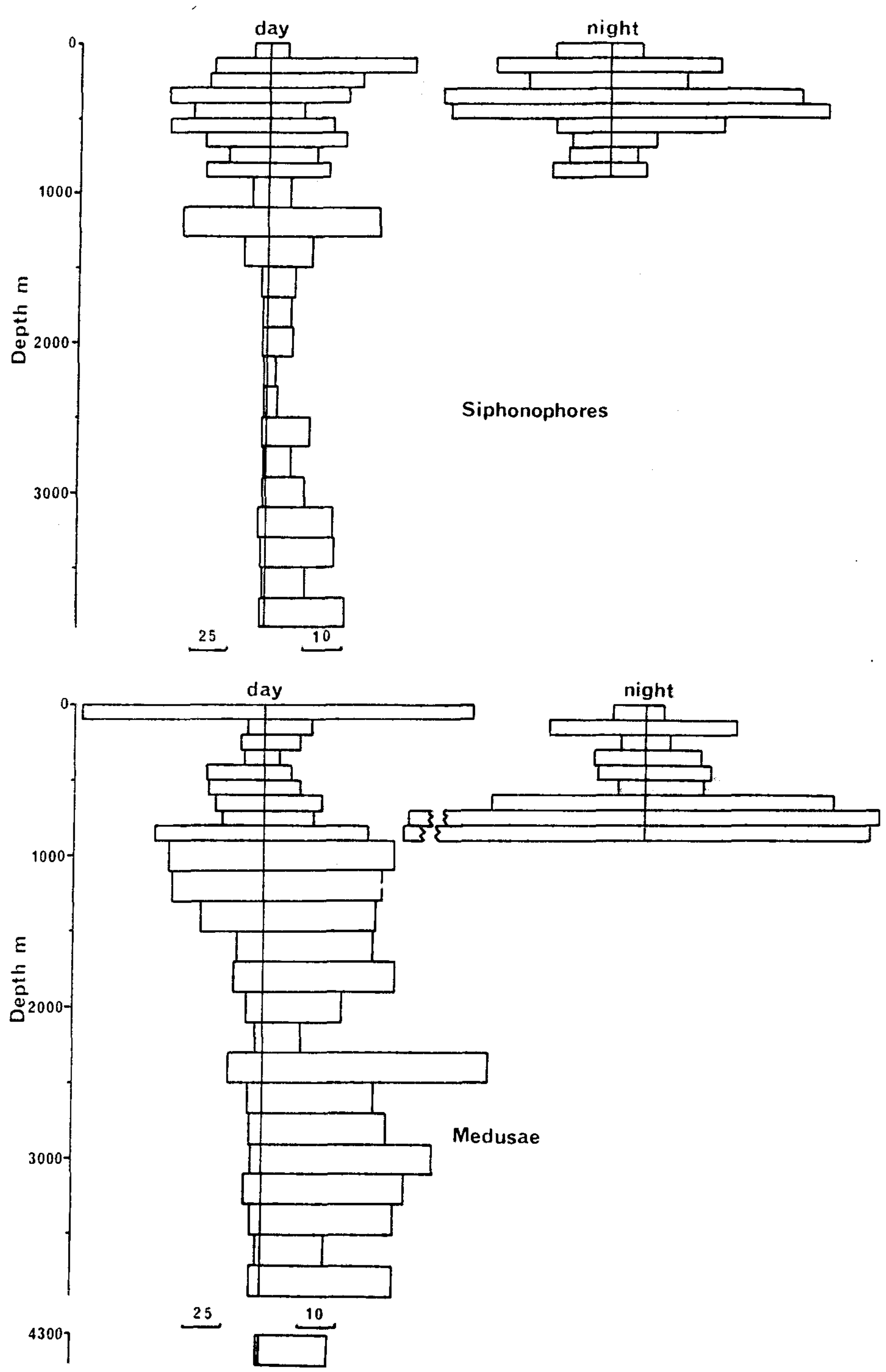


Figure 5. Vertical profiles of the dominant micronektonic groups taken at 42°N 17°W in May 1978. On the left the abundances per 10,000m^3, to the right is shown the percentage numerical contribution made by each group. Both day and night data are shown for the top 900m. (All from Angel and Baker 1979).

A. Siphonophores and medusae

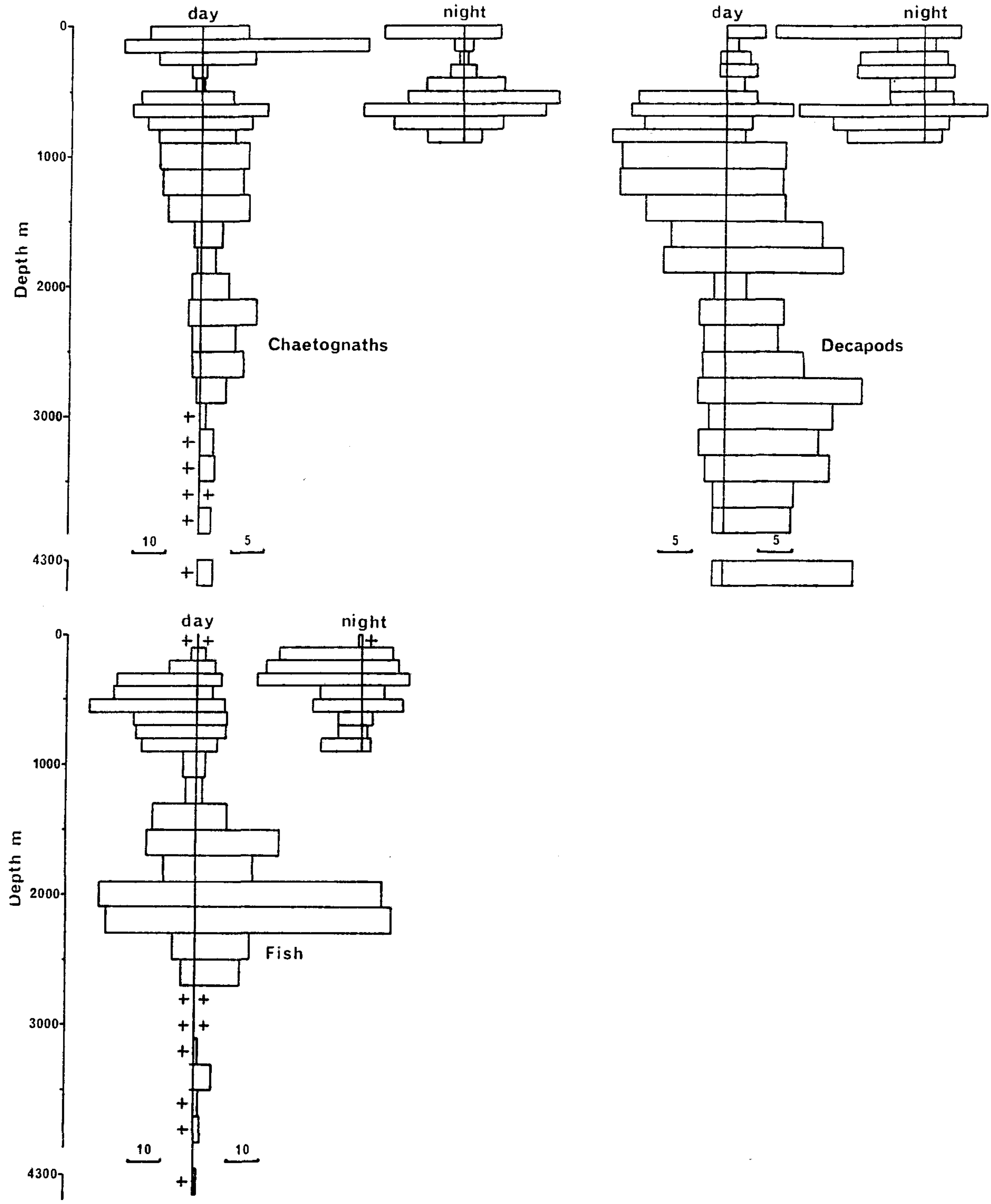


Figure 5. B. Chaetognaths, decapods and fish

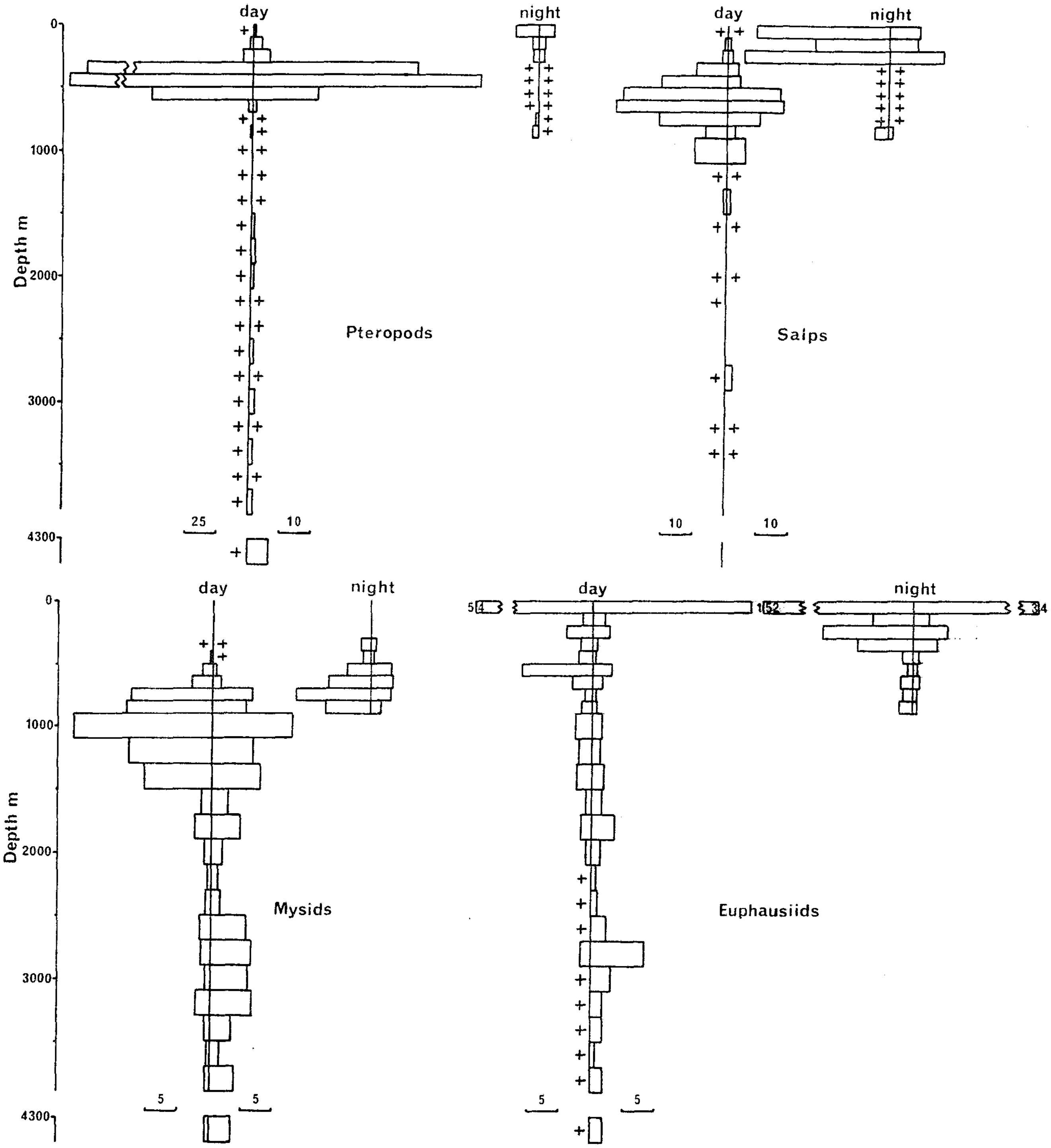


Figure 5. C. Pteropods, salps, mysids and euphausiids.

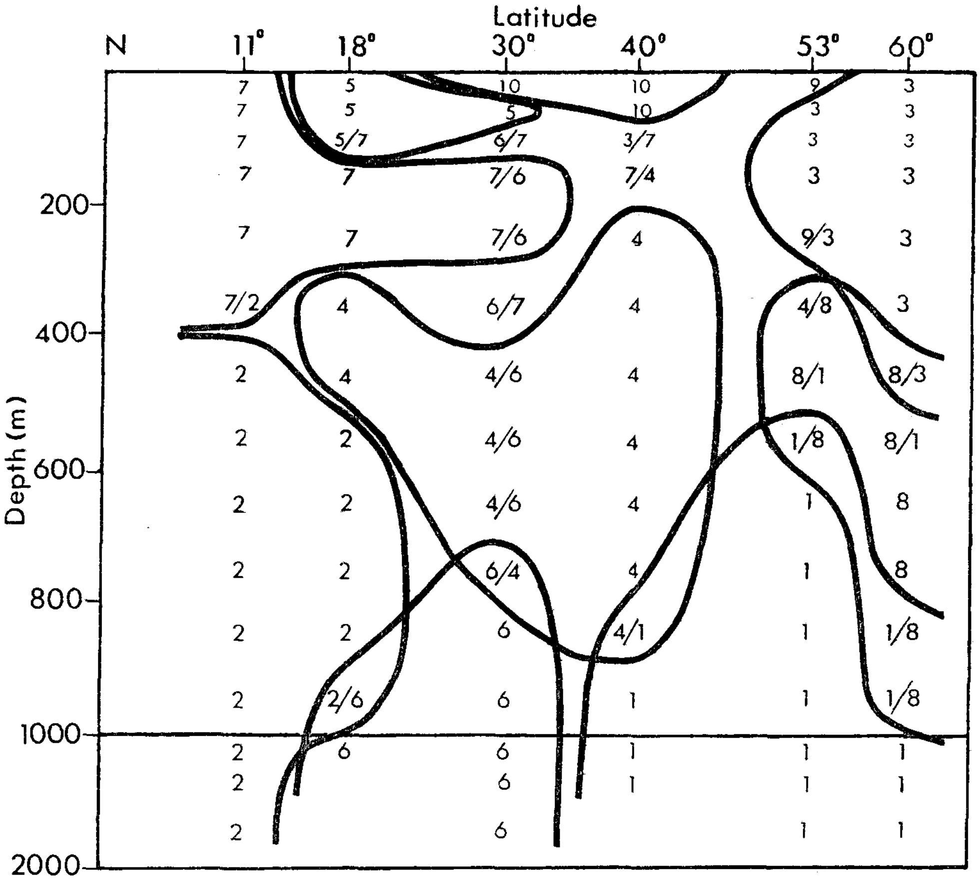


Figure 6. Vertical profile in the N E Atlantic of planktonic ostracod associations determined by factor analysis of a set of samples taken along a north south transect approximately along the 20°W meridian at 10° latitudinal intervals. (From Fasham and Angel, 1975).

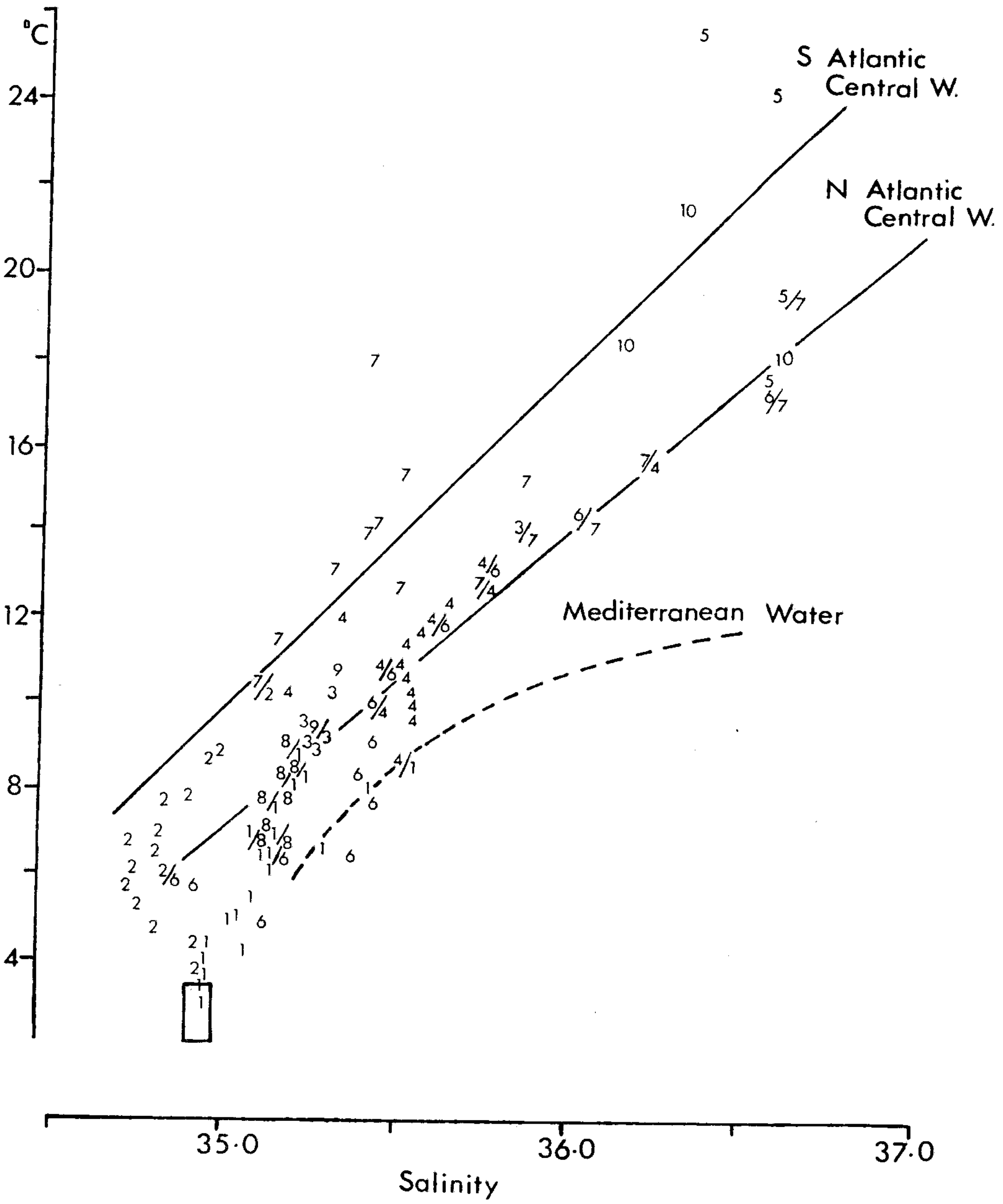


Figure 7. Plot of the various ostracod communities on the mean temperature - salinity value for each depth recorded along the transect shown in figure 6. (From Fasham and Angel, 1975).

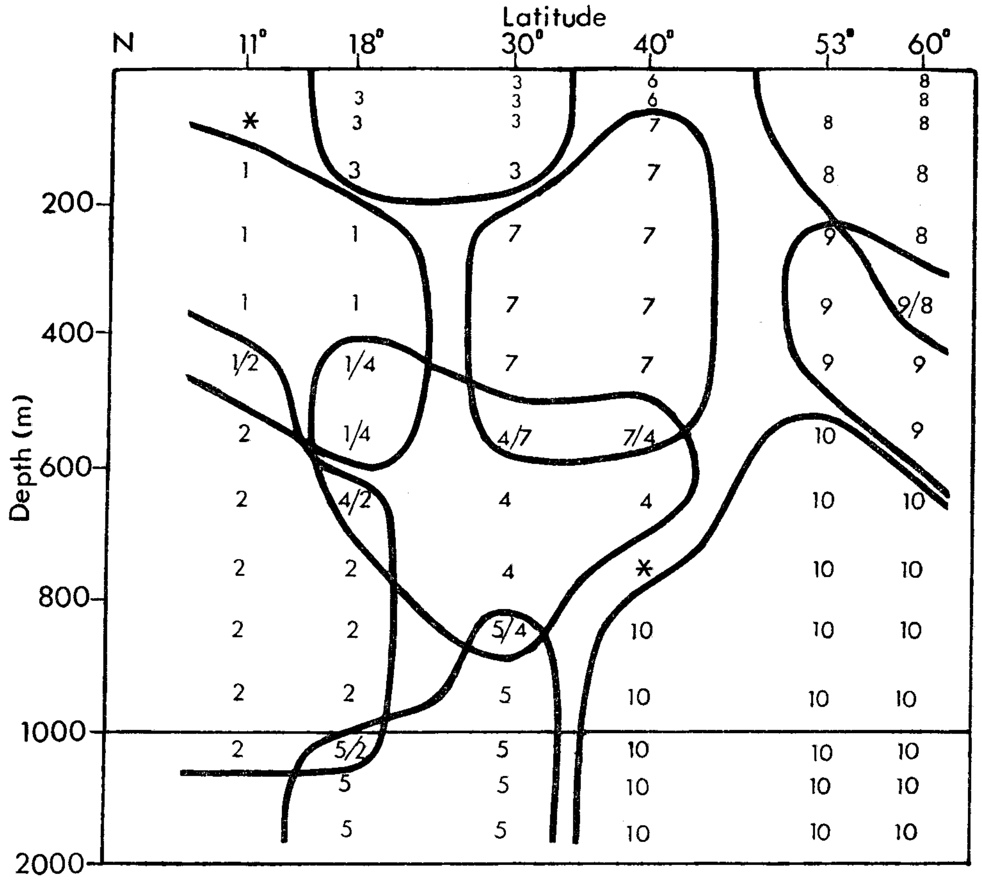


Figure 8. Vertical profile in the N E Atlantic of micronektonic decapod crustacean associations along the same transect as for the planktonic ostracods shown in figure 6 (from Fasham and Foxton, 1979).

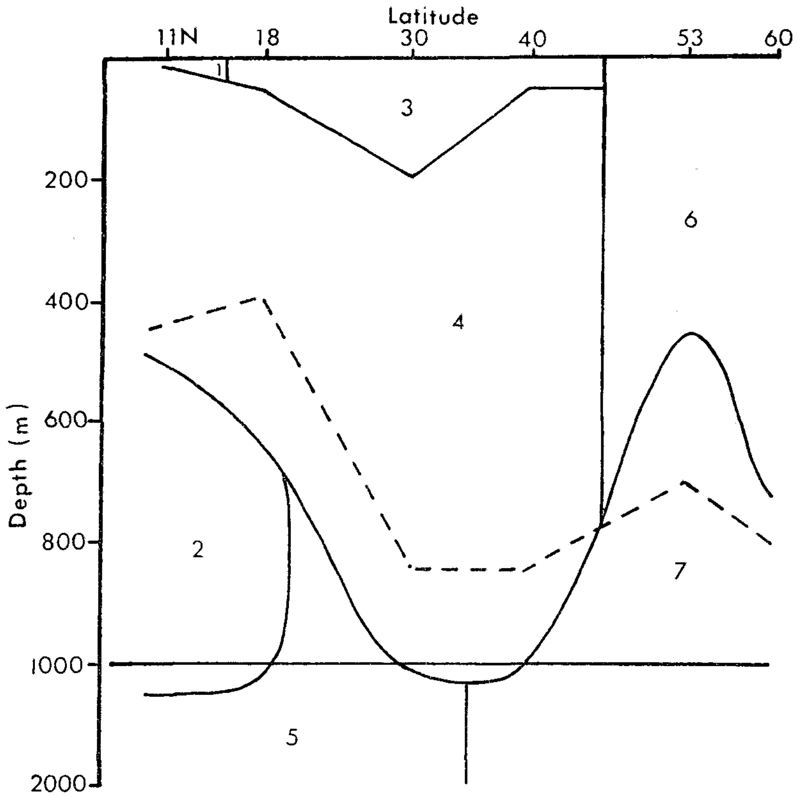


Figure 9. Postulated zonal boundaries based on the physical oceanographic criteria suggested by Fasham and Foxton (1979) and described in the text. The hatched line demarcating the lower boundary of zones 4 and 6 marked the depth of the oxygen minimum, whereas the continuous line follows the 8°C isotherm.

Figure 10. Diagrammatic scheme of the trophic relationships within the epipelagic, mesopelagic and bathypelagic zones.

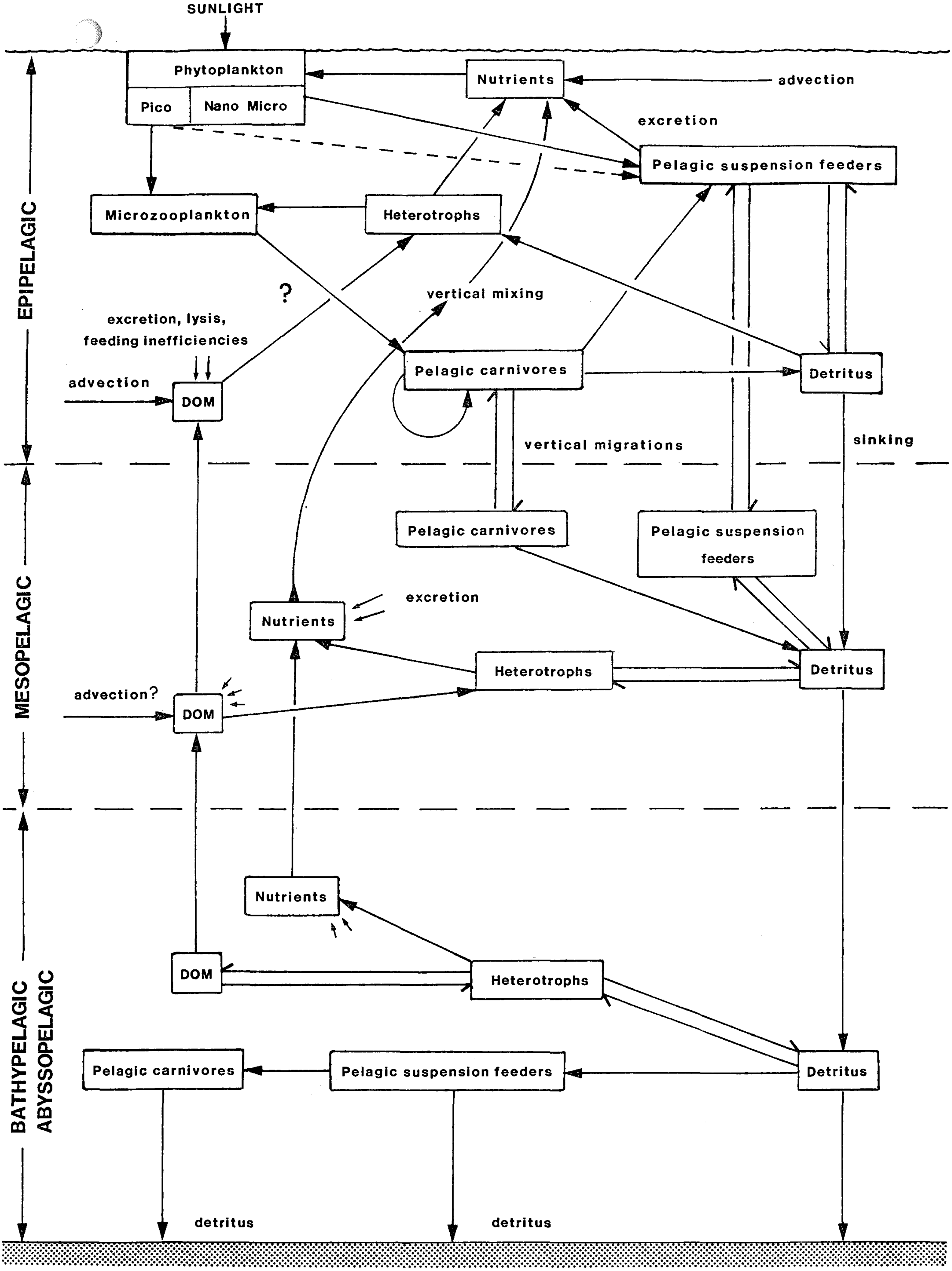
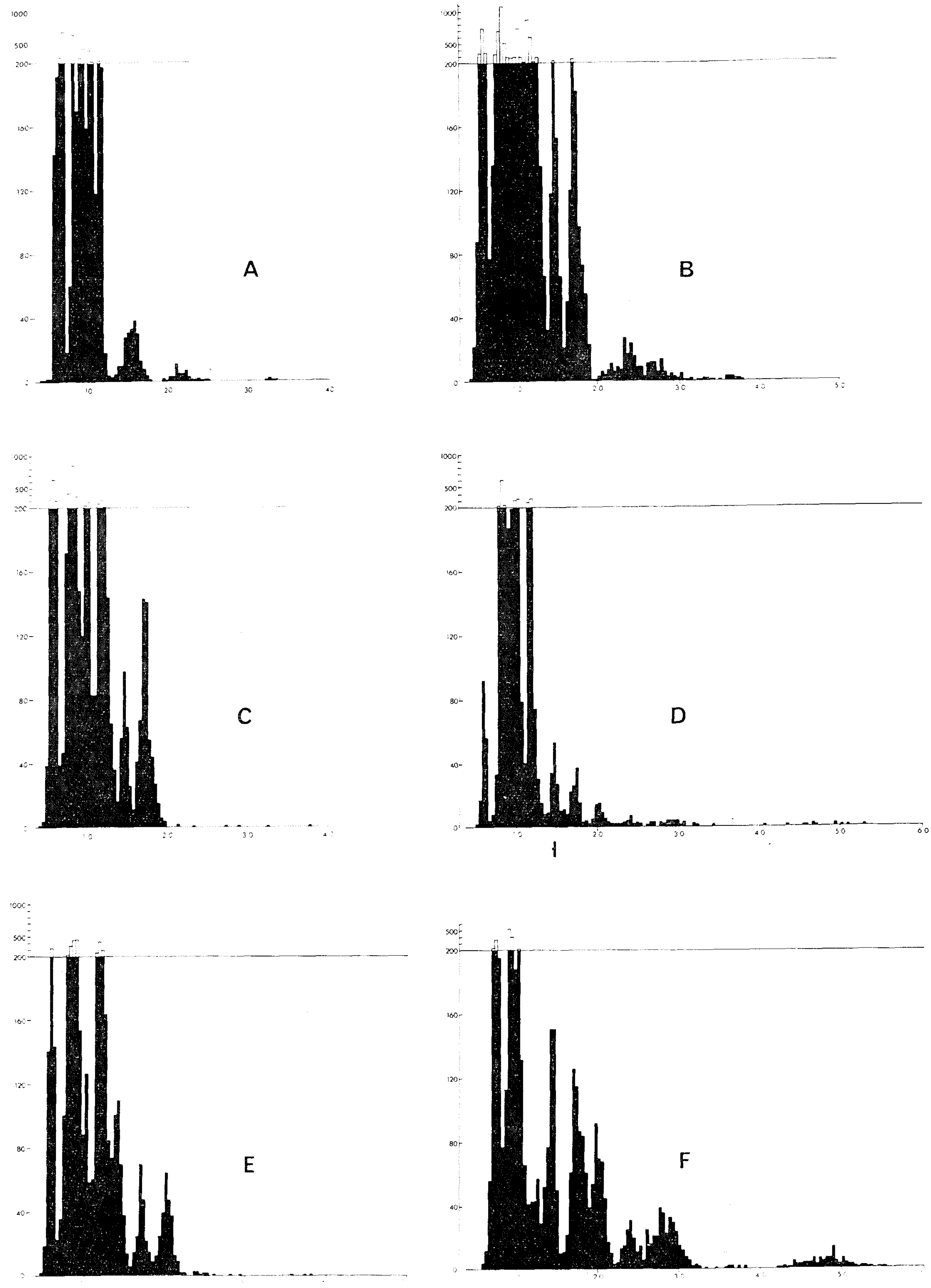

SUNLIGHT
Phytoplankton
Pico
Nano Micro
Nutrients
advection
excretion
Pelagic suspension feeders
Microzooplankton
Heterotrophs
?
vertical mixing
excretion, lysis,
feeding inefficiencies
advection
DOM
Pelagic carnivores
Detritus
vertical migrations
sinking
EPIPELAGIC
MESOPELAGIC
Pelagic carnivores
Pelagic suspension feeders
Nutrients
excretion
Heterotrophs
Detritus
advection?
DOM
BATHYPELAGIC
ABYSSOPELAGIC
Nutrients
DOM
Heterotrophs
Pelagic carnivores
Pelagic suspension feeders
Detritus
detritus
detritus

Figure 11. Population size spectra of planktonic ostracod communities sampled at 32°N 64°W near Bermuda in March 1973. Carapace lengths are in millimetres and the sample size has been scaled to make the volume of water filtered equivalent in all samples. Note that the vertical scale changes at >200. A. 100-50m Day; B. 100-50m Night; C. 300-200m Day; D. 300-200m Night; E. 400-500m Day; F. 600-700m Day. Note how the spectra are extended with increasing depth, and also at night as a result of diel vertical migration (from Angel, 1979).


1000
500
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120
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60
A
B
C
D
E
F

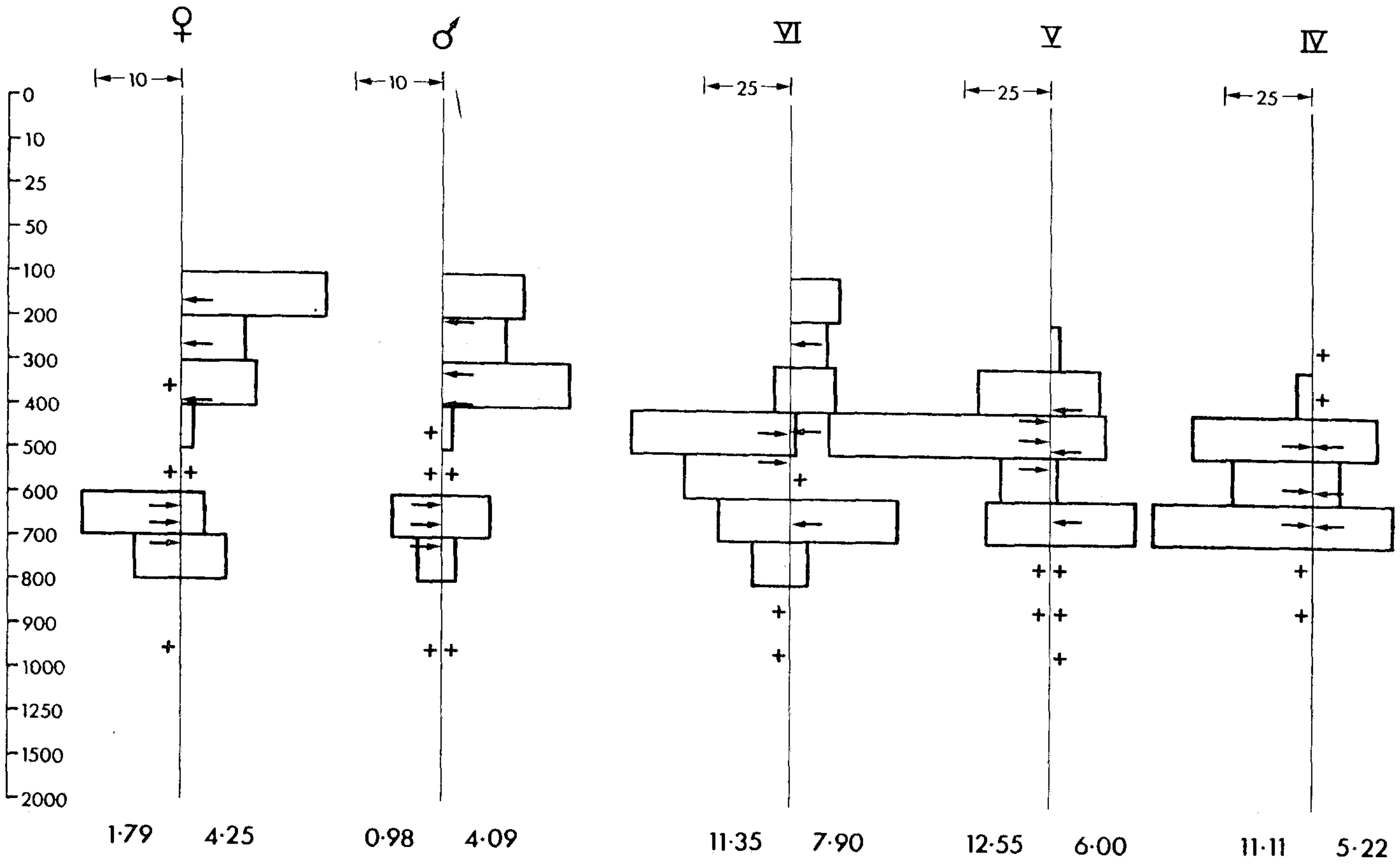


Figure 12. Abundance profiles (nos per 1000m^3) of the planktonic ostracod <u>Conchoecia imbricata</u> at 32°N 64°W near Bermuda in March 1973. Daytime distributions are to the left of the vertical axes and night-time distributions to the right. Profiles are given for males, females and the three oldest larval instars. The figures at the base of each profile indicate the number of each stage per m^2 of sea surface down to the maximum sampling depth of 2000m. The arrows indicate the quartile depths and + indicates abundances $<1/1000m^3$. Note the ontogenetic development of diel migratory behaviour (from Angel, 1979).

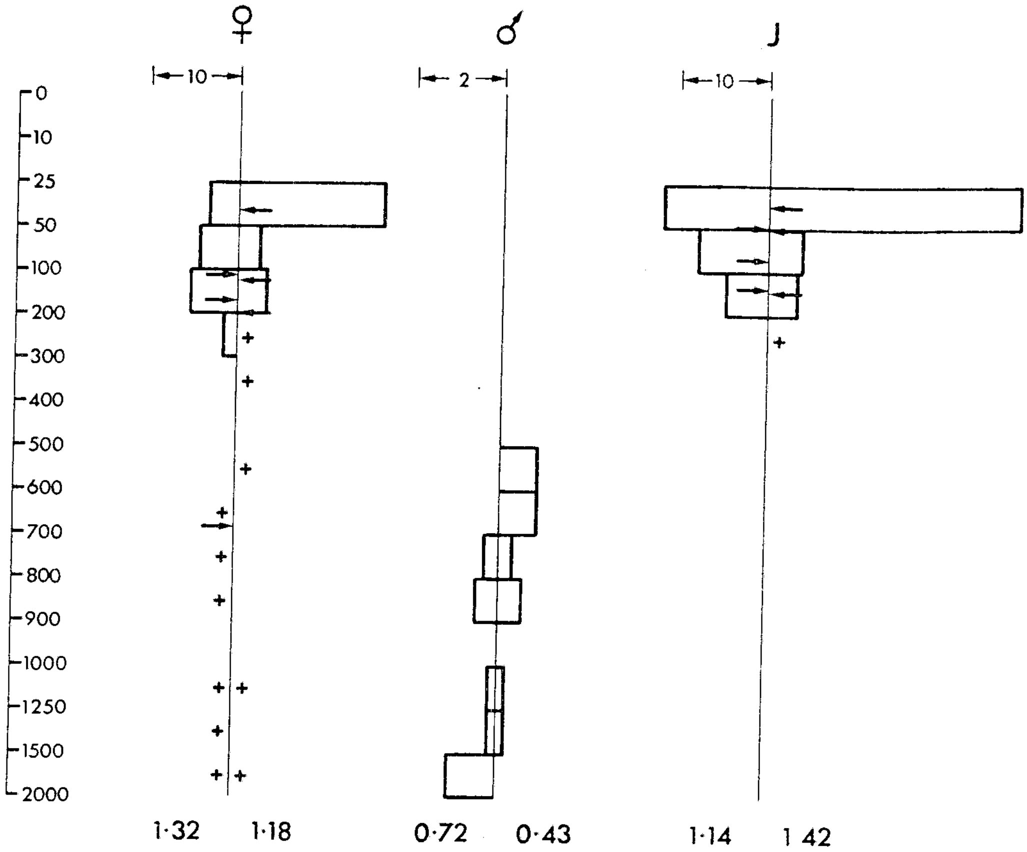


Figure 13. Abundance profiles (nos per $1000m^3$) of the planktonic ostracod <u>Halocypria globosa</u> at 30°N 23°W in April 1972. Daytime distributions are to the left of the vertical axes and night-time distribution to the right. Profiles are given for females, males and total juveniles. The figures at the base of each profile indicate the number of each stage per m^2 of sea surface down to the maximum sampling depth of 2000m. The arrows indicate the quartile depths and + indicates abundances of $<1/1000m^3$. Note the substantial depth separation between the main populations of males and females. (From Angel, 1979).

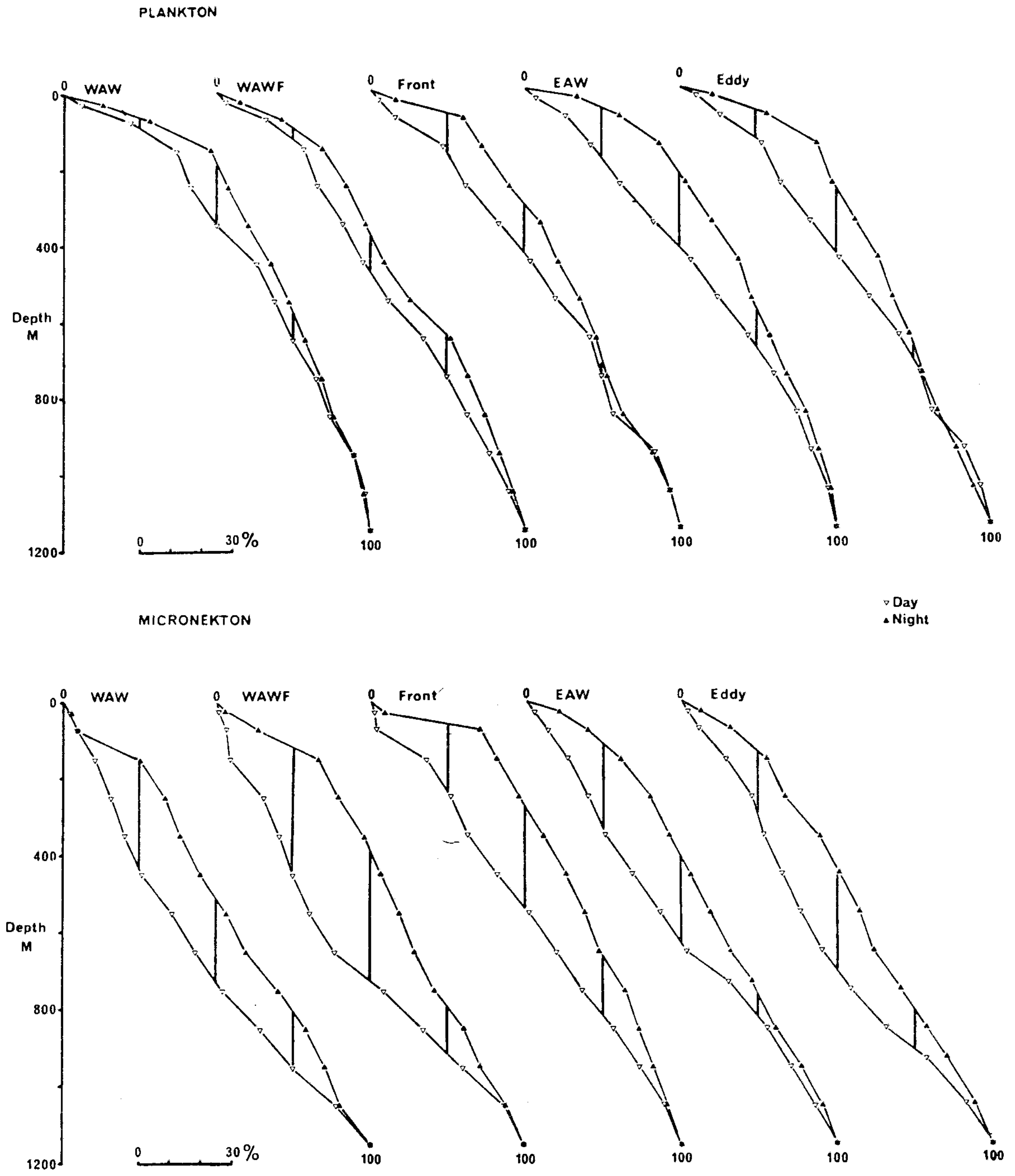
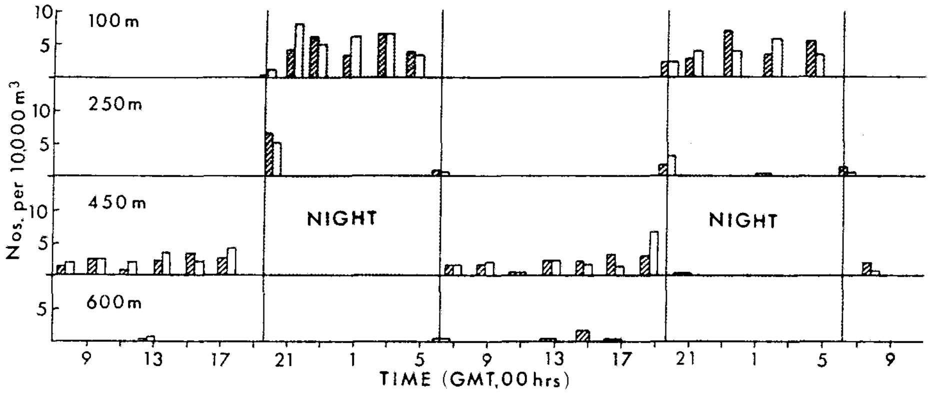
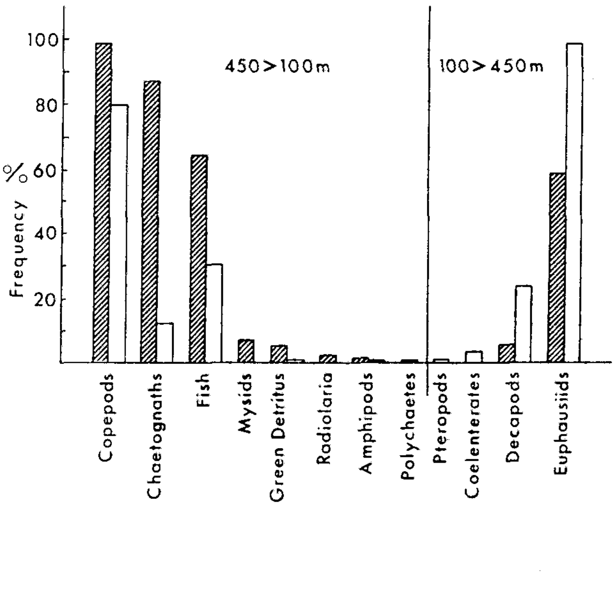


Figure 14. Biomass profiles for plankton and micronekton at five stations in the North Atlantic to the southwest of the Azores. Each profile is expressed as the accumulative percentage of displacement volume to a depth of 1200m. The vertical lines show the vertical shift in the quartiles (25%, 50% and 75%) between day and night. Note that in most of the day profiles day and night values were very similar to depths >800m, whereas the limit of 1200m does not encompass the total range over which diel vertical migration causes a shift in the distribution of micronektonic biomass. (From Angel, 1984).



A

Figure 15. Diel vertical migration in the micronektonic decapod crustacean Systellaspis debilis at 44°N 13°W in April 1974. A. Abundances in one hour horizontal tows of males (shaded) and females throughout four separate 48h periods at four depth horizons (100m 250m, 450m adn 600m) showing their patterns of diel vertical migration. B. Frequency of occurrence of prey items of Systellaspis debilis at 450m (shaded) and 100m (open). Items to the left of the vertical line were more frequency eaten at 450m than at 100m (after Roe 1984b).



B