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Large scale and mesoscale patterns of metabolic activity of epipelagic micro and mesoplankton in the Northeastern Central Atlantic at 21°N.

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ROSSBY or planetary waves are large-scale and long period, are generated due to temporal variations in the wind stress curl and they are produced annually in the central North Atlantic[1]. On the other hand, N_2 fixating organisms introduce the largest fraction of new nitrogen in the euphotic zone in tropical waters[2] and they must produce important consequences in the dynamics of the oligotrophic ocean. We present the results on plankton metabolism over a 2800 Km east-west section in the tropical North Atlantic Ocean showing a combined effect of Rossby waves and N_2 fixating organisms on the values of enzymatic activities of plankton in the <200, 200-500 and >500 μm size classes. While biomass values show only small increases westward at the surface layer (0-25 m), zooplankton enzymatic activities increases to the west part of the section where large phytoplankton chains were observed. Moreover, it is shown as the micro and mesoplankton index of metabolism at the seasonal thermocline layer, match the wavelength of Rossby waves observed. As higher zooplankton metabolic activity have important consequences in the flux of carbon in the ocean, productivity estimates of this low chlorophyll environments have to be reconsidered in relation to this two factors.

Subtropical gyres are one of the most stable areas of the ocean. The thermal and saline structure of the water column do not show drastic changes during the seasons. Low variations in the values of primary production and zooplankton biomass is the general trend in contrast with very high oscillations of temperate or inclusive equatorial areas where the different seasons and large scale divergences promotes variations in the thermal structure[3]. Those stable areas of the ocean gaves rise in the last decades to an important amount of literature about how works the productive system in relation to the vertical structure of the water column as a physical frame. Much work has been done about the relationship between location of the productive processes and the presence of subsurface chlorophyll maxima[4], the importance of new and regenerated production[5], the role of zooplankton in controlling the vertical structure of phytoplankton populations[6] and zooplankton vertical migrations as a mediatizing process in the vertical transport of organic and inorganic material in the ocean[7]. However, most of the work has been done in single locations where a typical and generalizable structure is going to deal with very large extentions of the ocean. In this context, it is of interest to point out the lack of information we have about the variability we can observe in short periods of time over large areas of high physical stability. A recent work[8] dealing with the biological effect of mesoscale and large-scale physical variability has opened the view that tropical oceanic areas are not as homogeneous as believed. Patterns of biological variability in relation to large-scale physical instabilities still remain unknown. Measurements of non-dynamic parameters such as chlorophyll-like pigments are not useful as they are subjected to predation in a day-night basis[9].

On the other hand, it has been shown recently the importance of N_2 fixating organisms in having a very important role in the primary production values in tropical waters. The diazotrophic cyanobacteria introduces the largest fraction of new nitrogen in the euphotic zone[2]. As zooplankton feed on this large phytoplankton chains[10], it is of interest to know the response of these animals in the presence of this food source in relation to the so-called central gyre and boundary areas of the ocean.

We have sampled a 2800 Km section perpendicular to the African coast at 21°N (Fig. 1) in order to study such a variability in micro and mesoplankton metabolism as an estimator of energy flux. We utilize enzymatic indices [electron transport system (ETS), glutamate dehydrogenase (GDH) and aspartate transcarbamylase (ATC)] to access variability in plankton metabolism and growth as there is no another way to obtain enough amount of data using classical procedures. We observe a high stable thermal structure in the upper 100 m with a seasonal thermocline between 50 and 75 m depth. Although we found a small deepening of this thermocline westward, it was not as patent as the one found at deeper levels (> 100 m). This is a typical situation of the boundary area between West Africa and the oceanic areas. In fact, we found lower salinities in the eastern part of the transect, giving rise to a two different areas representing boundary and central gyre conditions.

In Fig. 2A we have represented the thickness of the layer between the 15 and 18°C isotherme in dbars (≈ meters) after substracting the large-scale zonal gradient by means of linear regression. Anomalies of the potential energy should be observed by the thickness of this layer because it excludes completely processes like wind mixing and convection which start at the sea surface. We observed the presence of variations in the distance between the isothermes reflecting the presence of Rossby-wave-like-phenomena.These waves are generated in the eastern boundary of the ocean due to e.g., the time variations in wind stress and baroclinic/barotropic instability. We obseved a train of waves propagating westward. Visually, the zonal wave length was found to be determined in the range between 800-900 Km. Using a zonally averaged value for the radius of deformation of 48 Km from the belt placed between 20° and 40°W and 20° and 25°N[11] together with the observed zonal wave length of about 850 Km in the dispersion relationship of free Rossby waves, we obtain a serious hint for an annual period. Furthermore, if we accept the notion that the observed signal is a resonant oceanic response then we may speculate about a seasonal forcing in the area under consideration. We know from the literature that the annual course is the most energetic signal in the wind field in this region. In other words our findings are consistent with the results of models quoted above.

We measured zooplankton biomass as protein content in two size classes (200-500 μm and >500 μm) and we converted the biomass values according to the night/day (N/D) ratios obtained for the two size fractions. For the >500 μm size range we observed minimum values in the central part of the transect at the surface layer. This is a similar pattern to the one observed for the 200-500 μm in the same layer. At the deeper layers sampled, biomass was quite constant in the two fractions in all the transect.

Zooplankton ETS and GDH activities showed no differences in the N/D ratio in the two size classes studied at the different sampling depths. This is in agreement with the results obtained for the same ratio in the Canary Island waters[12] for ETS activity. This feature allow us to study the variability along the transect excluding the influence that vertical migration have in the surface layers. However, ATC activity displayed significant differences between day and night values. ETS activity shows (Fig. 2B) in the >500 μm size class at the thermocline level, a sucession of peaks which macht the wavelength observed for the Rossby waves. We found a lag of about 800-900 Km which is coincident with the wavelength of planetary waves observed and the range given in the literature[1]. We also observed this feature in the 200-500 μm in the same layer and at the surface values in the two size classes in the central gyre area, after substracting the westward increase in activity. This effect is also observed in average ATC activity in the >500 μm size fraction. Microplankton ETS activity at the seasonal thermocline level (Fig. 2C) show an inverse trend to the one observed for zooplankton ETS activity (Fig. 2B). As microplankton ETS activity is given in a unit-volume basis, highly related to biomass, we suggest that zooplankton is strongly controlling the microplankton community.

On the other hand, average values of ETS and ATC activity in the 200-500 and >500 μm fractions and GDH activity in 200-500 μm show an increasing trend westward from the middle of the section (Fig. 3). We grouped calanoid copepods in three different classes according to its size. We observed that in the surface layer (Fig. 4A), small calanoids (<1 mm) were diminishing from east to west reaching the minimun in the middle of the transect where we observed the minima in zooplankton biomass. It is expected to see small calanoids increasing in importance in central gyre conditions as the effect of an increasing role of small phytoplankton in oligotrophic waters. However, by the opposite, medium size copepods tend to increase westward (Fig. 4). The presence of large phytoplankton chains promotes the increase of non-small calanoids.

In warm-water oceanic areas, the velocity of processes related to the transfer of energy in the different trophic levels is high and the flux must be conducted to the microbial loop and zooplankters without delay. For these reason, it is commonly to observe very small values of chlorophyll and of primary production in this areas[8,13]. The lack of a phytoplankton specific productivity method do not permit us to see the effects of physical instability and its variability effect in the biological system. In that way, zooplankton indices of metabolism and growth can show us the ultimate result of an increase in phytoplankton specific production because it controls, at least in part, the growth of autotrophic organisms. Along these lines, we have observed severe variations in the parameters we measured in our section. Two main causes can be cited as the causative mechanism of increased zooplankton activities. In one hand, the magnitude of metabolic processes is not lower in the central subtropical gyre than in the boundary area of the ocean. We have good evidence of increased activity to the western part of the transect where we observed large phytoplankton chains. The subsampling effect on the diazotrophic cyanobacteria has underestimated primary production in this large areas of the ocean. The fact that mesozooplankton feed directly on these chains[10] and the importance of processes related to N_2 fixation is corroborated by our data in the presence of higher zooplankton activity.

On the other hand, our observations suggest a high degree of probability that Rossby-wave-like-phenomena, which could be seasonally forced in the east, zonally change their conditions in potential energy with a wave length of about 850 Km and clearly influence the hydrographic environment of micro- and mesoplankton along our extended zonal section. The higher zooplankton ETS activity at the level of the seasonal thermocline coincides with the smaller distance between the isothermes considered. If the distance of isothermes at the seasonal thermocline level are related to the observed at deeper levels, it is easy to elucidate that as water transparency increases westward, the euphotic zone is deeper, allowing to reflect the Rossby waves biological effect more patent in the central gyre area. We also believe that processes involved in the increases in activity are quite complex. They are related to the mesoscale eddy-like structures produced by the wave associated presure instability and the lag produced in biological systems between different trophic levels.

There can be no doubt that, in a dayly basis, zooplankton vertical migration is the most important phenomenon in relation to variability in the oceanic epipelagic areas as has been described in the past. However, instability of the water column as the one described above and the presence on N_2 fixating organisms could produce important effects in the values of dissolved and particulated carbon being transported to the mesopelagic domain by zooplankters. Because the zooplankton is one of the ultimate mediators in the biological effects of physical instabilities in warm-water ecosystems, the value of chlorophyll-like pigments from satellite data to obtain productivity values must be regarded with caution when big numbers are extended to vast areas of the ocean. The now almost classical picture of very low phytoplankton values in central subtropical gyres of the North Atlantic Ocean taken by Coastal Zone Color Scanner must be reconsidered in terms of biological productivity. While in equatorial areas, grazing and low Fe amounts limitate primary production[14], in the tropical area the bad sampled N_2 fixating organisms and the grazing effect can modify the previous knowledge we have about biological functioning of tropical systems. Moreover, Rossby waves enhance and/or promote increased productivity in those areas and must be taken into account when studies of time series in the tropical or subtropical oceanic areas are undertaken. In trying to explain biological variability such a pattern of biological instability can produce background noise in the data which can originate serious troubles in interpreting trends over time.

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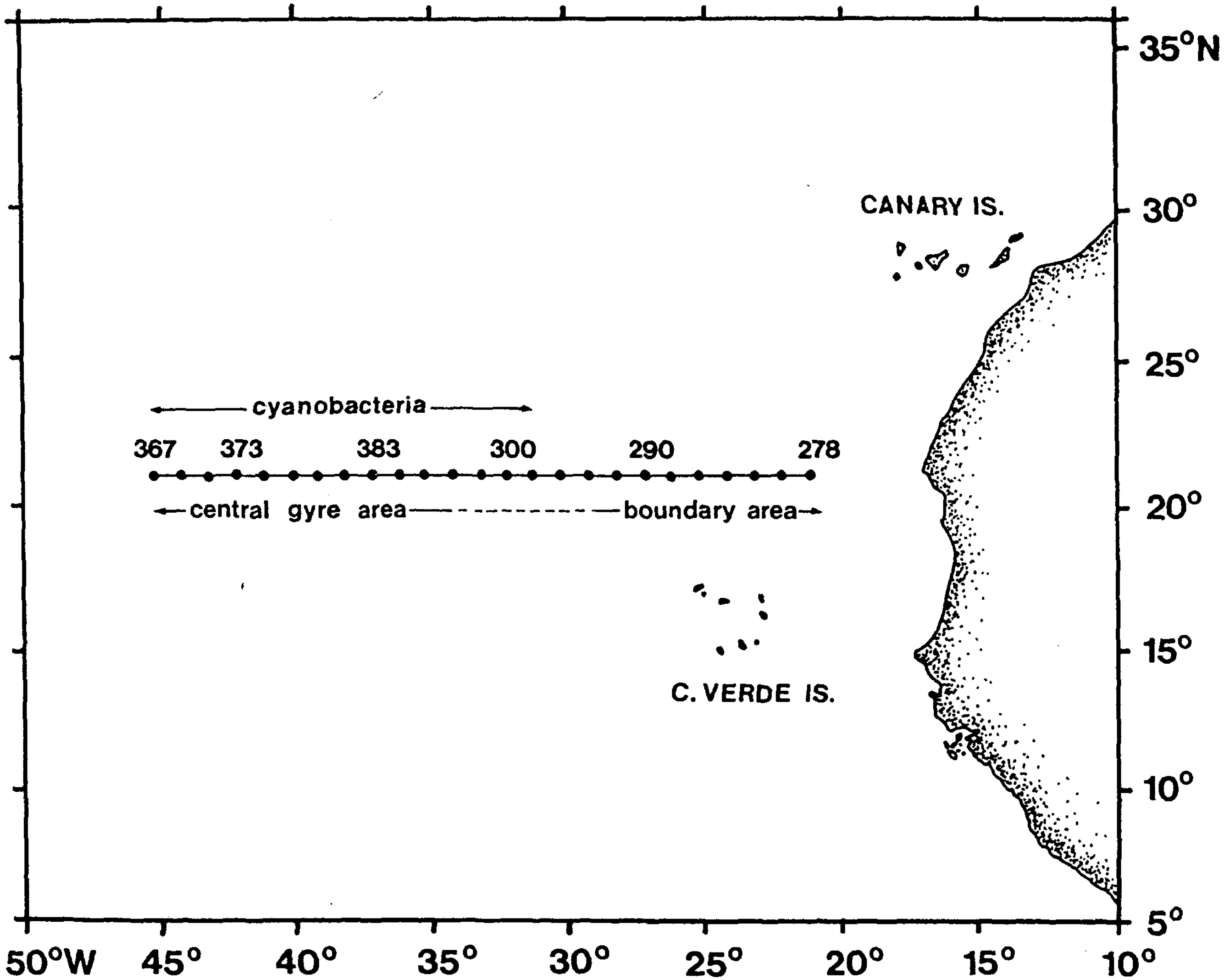
FIGURE LEGENDS.

Fig. 1.- Location of oceanographic stations in the North Central Atlantic. The research cruise was conducted in September 1989 and biological sampling was caried out every 60 miles. Indicated boundary and central gyre conditions are based on temperature and salinity data. Presence of cyanobacteria chains is also indicated as observed from plankton net catches.

Fig. 2.- Comparison of the deviations of (A) the distance between the 15 and 18°C isothermes after substracting the large-scale zonal gradient, (B) Mesoplankton ETS activity in the >500 μm at the seasonal thermocline level, (C) ETS activity in microplankton at the seasonal thermocline level. We considered 25, 50 and 75 m samples. The phytoplankton chains were excluded because the sampled was poured through a 200 μm mesh net. ETS activity in (C) has been calculated after substracting the increasing eastward trend in activity. The superimposed line in A, B and C is the smoothed representation of data (histograms). Note that ETS activity in microplankton and zooplankton present clear peaks in the central gyre area, with a lag of about 900 Km coinciding with the annually generated Rossby waves and they have, in all the transect, an inverse relationship indicating that zooplankton is controlling microplankton community.

Fig. 3.- Average specific ETS, GDH and ATC activities (A, B and C respectively) in the 200-500 μm and >500 μm size classes. ATC activity has been corrected for differences between day and night values. Observe the westward increase in activity in the central gyre area coinciding with the presence of large phytoplankton chains.

Fig. 4.- Copepod density (A) at the surface (0-25 m) and (B) at the seasonal thermocline (25-75 m) layers. The two sizes considered were <1 mm (solid line) and 1-2 mm (dashed line), representing small and medium size copepods. Big copepods (>2 mm) were present in very low densities showing no patterns in their distribution along the transect. Cyclopoid number increased gradually westward at the surface layer as expected to observe from boundary to central gyre conditions.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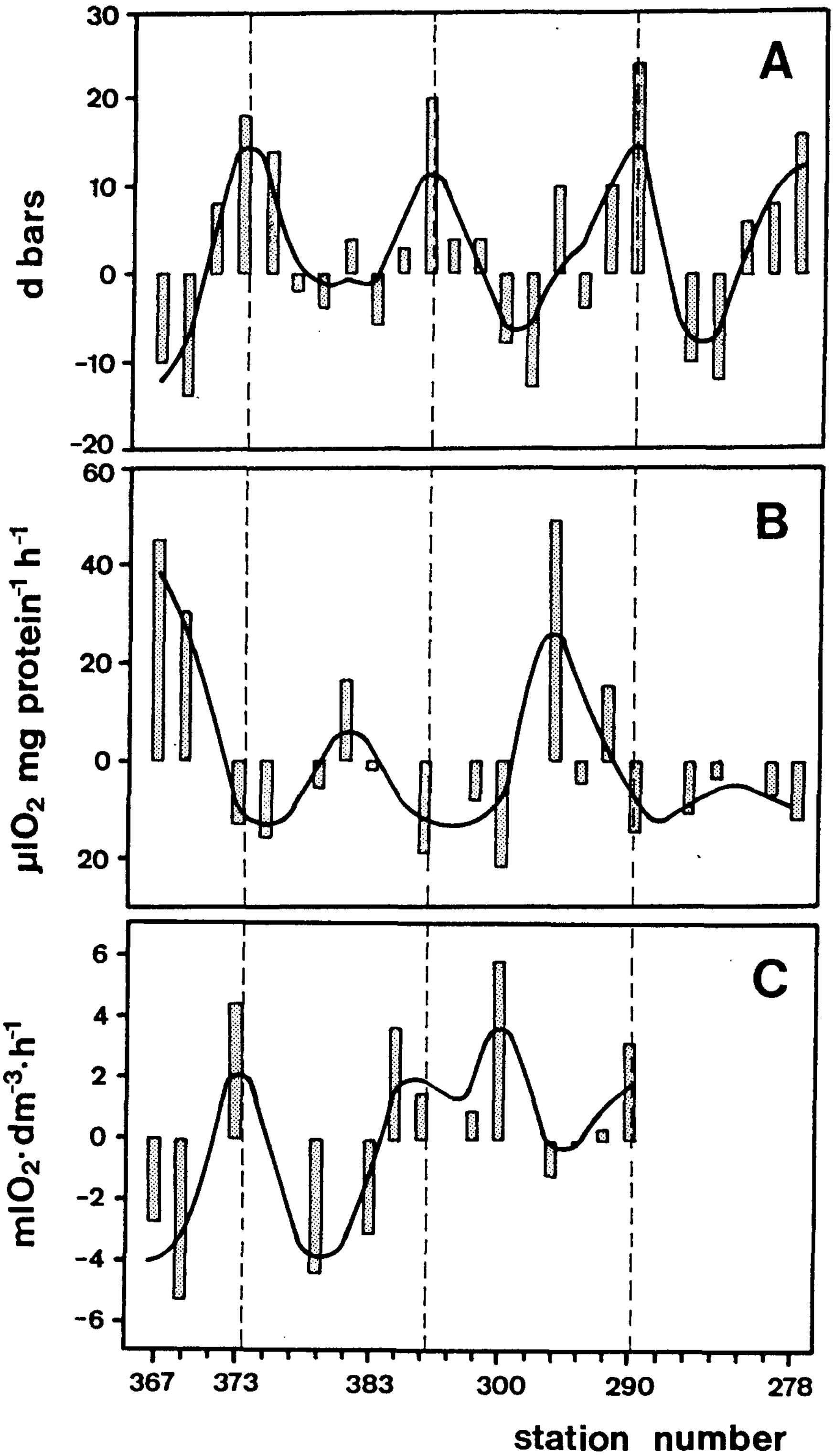

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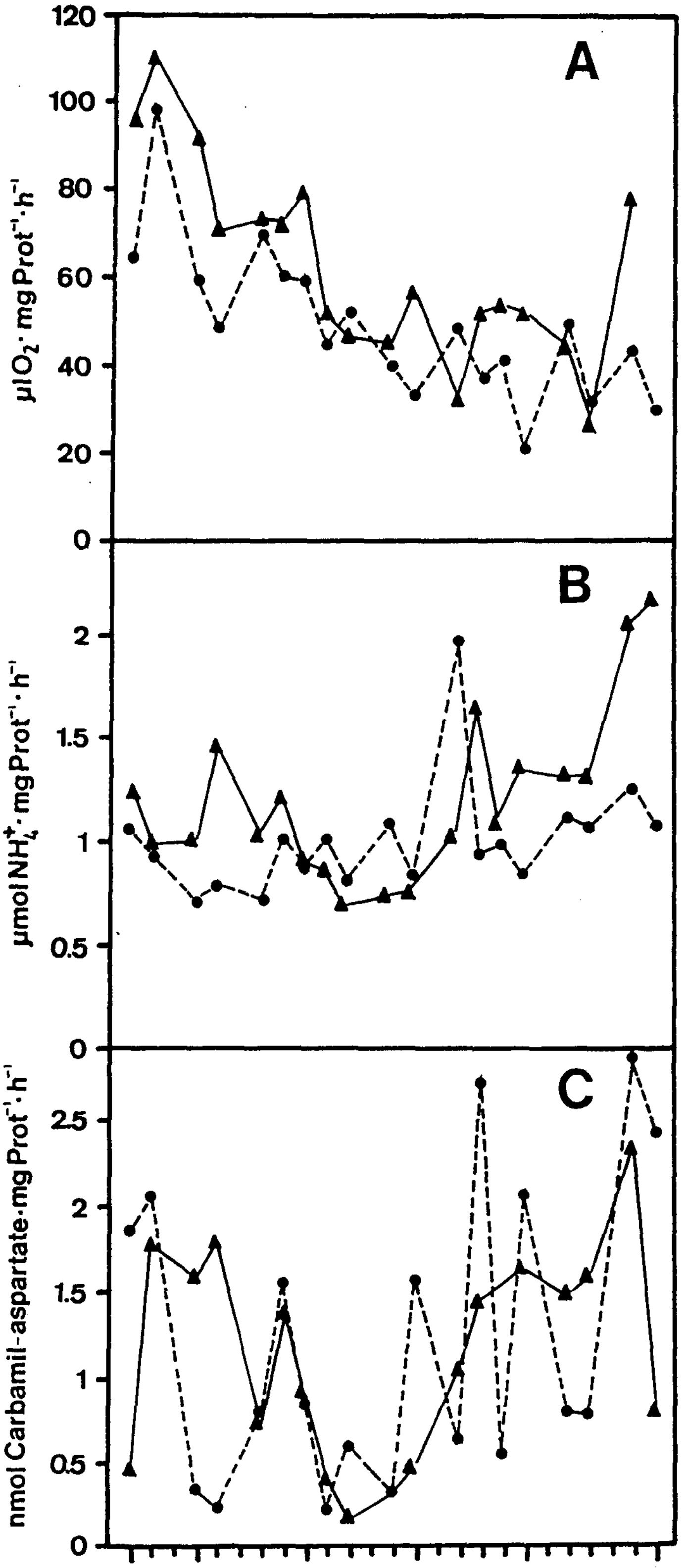
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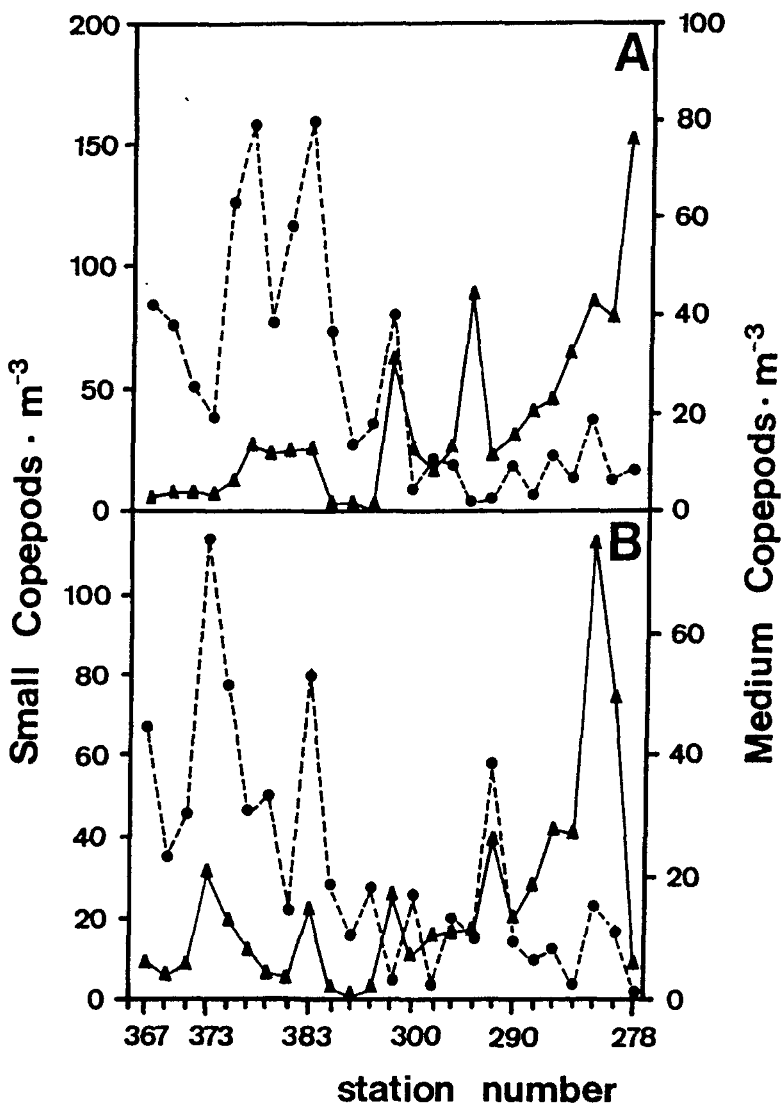
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