NERITIC ZOOPLANKTON SUCCESSION STUDIED WITH STATISTICAL ENTROPY MEASURES: THE ROLE OF SPACE AND THE HIERARCHICAL MATCHING OF THE ENVIRONMENT

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SUMMARY

Succession in neritic zooplankton is studied, and the role of space and hierarchic adaptation to the environment assessed. Four stations located at the vertices of a square with sides of 1.5 miles, off Tarragona (Western Mediterranean), at depths between 20 and 50 m, were sampled from October 1984 to October 1985. Hydrographical data were obtained and zooplankton was caught by oblique hauls; copepoda were classified to the species level and the individuals were counted, as well as those belonging to other groups.

Two disturbances (perturbations) were identified in March and June, which gave rise to various successional events. The process has been studied by computing entropies, taking into account the space (conditional probabilities),which allowed us to calculate the contribution of space to total entropy, and the mutual information between space and populations. These calculations were performed separately for the copepoda populations and for the rest of zooplanktonic groups.

Evidence is given that during a successional episode initiated by a perturbation, relative mutual information between the space and the populations rises abruptly at the beginning and decreases slowly afterwards, until the next disturbance, while the maximum total entropy is obtained approximately two months after the beginning of the process. There is a time lag between the maximum of relative mutual information calculated for copepoda and that calculated for the groups of zooplankton. Taken together, this suggests that during succession, plankton structures itself hierarchically, it being possible to identify two steps in each episode: the first one is directed by external energy, the second is directed from the system itself. During each successional episode, the specific composition of the populations of copepoda changes continuously, but at a decreasing rate, while higher order taxonomic groups remain fixed in the first step but change in the second.

INTRODUCTION

MARGALEF (1958) described the general trends of marine phytoplankton succession and unified some concepts by relating them to terrestrial succession (MARGALEF, 1963). He also proposed the selection of phytoplankton life-forms during succession in an unstable environment (MARGALEF, 1978) and recently (MARGALEF, 1985), he put more emphasis on the spectra of disturbances that generate pulses of successional events, which might generate chaos in any model of marine populations (MARGALEF, 1986).

According to MARGALEF (1985, 1986), energy in ecosystems is continuously being converted into organization and information. External energy enters the system in an irregular way, at more or less disjointed centers and with different intensities. Each input of energy or disturbance starts an ecological succession and stops or resets the one that was in action. This resetting from outside remains unpredictable from inside the system and imposes small or large retrogressions in the degree of organization. As energy from an external input decays, spatial organization of the system develops, and although the system is governed and punctuated by inputs of external energy, it is expected that the process of ecological succession at any given place may follow predictable regularities.

Among the characteristics which change during succession (MARGALEF, 1968, 1974; ODUM, 1971), most attention has been given to the variation in species composition. It is also the only effect that can be studied without hypothesizing about the holistic behavior of the system; and so it is the minimum definition of ecological succession.

MARGALEF (1957) introduced the use of statistical entropy in ecology as a tool for measuring species richness or diversity, assuming that the set of species is a communication channel (SHANNON & WEAVER, 1949), and that its capacity in bits per individual may be calculated on the basis of species frequencies in the samples. In this way, the information per individual gives an idea of the width of the biological communication channel (MARGALEF, 1961), which depends on the system of codification used by the biologist (most of the time, species are used and individuals are considered to be interchangeable within the same species). The Shannon diversity measure (mostly in a spectral formulation) has been used since then in many ecological problems to study the spatial complexity of a system or to compare maturity stages within the successional process (MARGALEF, 1961, 1962, 1969a, 1969b, 1974, 1975; PIELOU, 1969, 1975). In the last decade the theory of communication and the concept of statistical entropy have been widely used in the study of systems complexity and self-organization, as well as in marine ecology (ATLAN, 1985; MARGALEF, 1985; CONRAD, 1983, 1985; ULANOWICZ, 1986). However, this does not prevent Margalef writing that "In my experience there is a widespread and noticeable dislike for the concepts of diversity and succession, expressed by ecologists who are otherwise fond of statistical approaches and claim to be the genuine reductionists" (MARGALEF, 1989).

In the present paper we analyse the temporal seasonal evolution of statistical entropy of zooplankton and the contribution of space in total entropy, from the winter-spring phytoplankton bloom to the end of the summer, in a neritic Mediterranean area, on the NE coast of Spain. Two disturbances or inputs of energy were identified that were followed by a process of succession. During succession, energy decays and is transmitted from the lower levels (primary producers), through the herbivores, to the higher levels in the zooplankton. This flux of energy helps the organization of the biological system made up of organisms of different types and species. From the point of view of quantity, energy input is followed by an increase of biomass. First of all, there is an increase in chlorophyll, which may be viewed as the actual disturbance for herbivores. Animal biomass may then be considered as the input for higher order trophic levels. The decay of energy gives way to an increase of species diversity and spatial structuring if the physical environment is stable enough. In consequence, there is an adherence between environment and plankton that is transmitted hierarchically (MARGALEF,

1961; LEVASSEUR *et al.*, 1984). In the present study we have not attempted to measure anything like a statistical entropy of environment (ATLAN, 1985), which could have helped a close analysis of the hierarchical transmission of spatial structures from the environment to the biological sphere. However, we have compared the evolution of the statistical entropy calculated in the group of copepoda (classified into species) and the whole zooplankton (classified into higher order taxonomic groups), looking especially at the contribution of space. Mutual information between space and taxonomic composition of organisms is displayed and interpreted.

MATERIAL AND METHODS

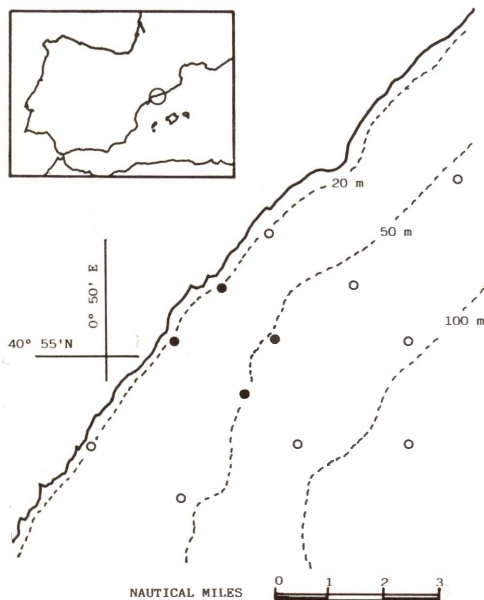### THE DATA

Hydrographic and zooplankton data used

FIGURE 1. Geographical situation on the NE Spanish coast of the four stations analysed in the present paper (black dots), in the frame of the whole sampled grid (open circles).

here were obtained in a series of cruises (PENTA) carried out by the Instituto Español de Oceanografía. Twelve stations covering an area of some 30 km² on the Catalan continental shelf (Western Mediterranean, NE coast of Spain), were sampled from October 1984 to October 1985. Four of the stations (at depths between 20 and 50 m) were sampled eleven times, while the others were sampled every two or three months. The frequency of sampling was higher from March to the end of the summer, and lower in winter (the longest gap was between December and March). In this study we present the analysis of the data obtained in these four stations, which were situated in the vertices of a square with a side of 1.5 miles (Fig. 1).

Zooplankton was caught by oblique hauls, using nets of 250 μm mesh. Copepods were identified at the level of species, when possible, and counted (87 species or items). Other major groups were classified at higher taxonomic levels (18 groups), and counted (Tables I and II).

The small scale (1-10 km) structure of phytoplankton in the neritic waters of the NE Spanish coast has been studied by MARGALEF (1969a) and ESTRADA (1979), but there are no comparable studies of zooplankton in the same area. The most complete study of the neritic zooplankton in the area is the one by VIVES (1966). A good summary of the annual zooplankton cycle in the neritic waters of the NE coast of Spain can be found in ESTRADA *et al.* (1985).

Previous studies concerning zooplankton in the NW Mediterranean that implied a temporal high frequency sampling did not take space into account (e.g. IBANEZ & DALLOT, 1969) and a recent work that implied high frequency sampling in space could not resolve intermediate scales between daily and seasonal variability (BOUCHER *et al.*, 1987). In fact, plankton dynamics is now being more often studied in relation to hydrodynamics (LEGENDRE & DEMERS, 1984; ROTHSCHILD, 1988;

TABLE I. Mean number of individuals per cubic meter in the four stations studied of those species of copepoda that represented more than 1 % of the copepoda population, at some time during the sampling period. Those species indicated by sp. were not adult individuals. The number of indetermined copepodites are also shown.

Copepoda species	1984 Oct	Dec	1985 Mar	Apr	May	May	Jun	Jul	Aug	Sep	Oct
Calanus helgolandicus	0	1	0	11	15	41	48	13	0	0	0
Calanus sp.	11	3	2	3	12	0	0	0	1	0	1
Mecynocera clausi	0	0	0	0	0	10	0	0	0	0	0
Paracalanus parvus	96	12	26	68	42	125	439	209	12	21	10
Clausocalanus arcuicornis	76	11	0	0	4	7	10	10	2	1	3
Clausocalanus furcatus	3	2	0	0	1	0	5	0	7	1	0
Clausocalanus pergens	0	0	0	1	79	8	65	4	45	57	94
Clausocalanus sp.	9	1	271	2	10	9	24	9	25	7	7
Ctenocalanus vanus	1	14	170	3	36	2	9	2	0	0	
Diaixis hibernica	1	3	0	0	2	0	0	0	0	0	0
Temora stylifera	185	72	0	0	0	0	1	25	63	263	209
Pleuromamma sp.	0	10	3	0	0	0	0	0	0	0	0
Centropages typicus	6	0	24	4	25	72	197	15	0	0	1
Centropages violaceus	6	0	0	0	0	0	0	0	0	1	1
Centropages kroyeri	0	0	0	0	0	0	0	22	6	29	0
Centropages sp.	6	0	0	0	0	0	0	0	0	0	0
Isias clavipes	9	1	0	0	0	0	0	0	0	5	2
Acartia clausi	12	28	32	23	13	33	10	100	5	21	12
Acartia latisetosa	0	0	0	0	0	0	0	3	4	1	2
Oithona plumifera	60	45	8	4	7	1	2	3	9	36	96
Oithona helgolandica	3	1	11	24	29	108	58	48	0	1	0
Oithona nana	1	0	0	0	0	0	14	244	1	0	
Oithona sp.	17	3	2	0	0	0	0	0	0	0	0
Oncaea sp.	17	13	2	0	0	0	0	0	0	0	0
Corycaeus flaccus	0	3	0	0	0	0	0	0	0	0	1
Corycaeus latus	3	6	0	0	0	0	0	1	14	12	10
Corycaeus brehmi	0	2	5	1	4	0	0	1	2	3	1
Corycaeus furcifer	0	3	0	0	0	0	0	0	0	0	0
Corycaella carinata	12	2	0	0	0	0	0	0	0	0	0
copepodites indet.	16	7	15	6	9	9	14	10	4	8	5

LEGENDRE & LE FÈVRE, 1989), but space-time scale problems are difficult to solve in practice.

In the sampling region, currents along the coast at 20 to 50 m depth are of the order of 10 cm s^{-1}, changing their direction irregularly. The net flow ranges from 5 cm s^{-1} on the surface to 1 cm s^{-1} at 50 m depth (FONT, 1983). Sampling on the vertices of a square with a side of 1.5 miles ensures that one is not sampling the same body of water in the interval of a few hours, while gathering the spatial variability linked to internal and inertial waves and horizontal turbulent patches (e.g. DICKEY, 1988). On the other hand, the temporal sampling intervals (less than one month on average between March and October 1985) seem appropriate for examining the seasonal successional evolution of zooplankton (e.g. STEELE, 1988).

MEASUREMENT OF ENTROPIES

The basic expression for the measurement of entropies in each sampling or cruise considers the species (or zooplanktonic groups) and the geographical positions as the two sources of total statistical entropy, so that total and marginal frequencies are used in the calculations. The relationship among the different entropy measures is given by:

$$HT = HP + HS/P = HS + HP/S,$$

TABLE II. Mean number of individuals per cubic meter in the four stations studied of the more frequent zooplanktonic groups.

Zooplankton group	1984 Oct	Dec	1985 Mar	Apr	May	May	Jun	Jul	Aug	Sep	Oct
Medusae	3	5	23	56	12	9	1	2	2	1	1
Siphonophora	26	56	23	785	75	136	153	187	13	37	27
Copepoda	552	254	582	154	299	428	904	735	211	472	474
Cladocera	424	12	4	3689	231	1646	231	4167	216	155	38
Ostracoda	1	11	0	2	1	1	1	1	0	0	0
Chaetognatha	32	52	0	3	5	3	5	61	8	30	29
Pteropoda	5	3	0	11	21	19	1	0	1	0	13
Appendicularia	71	98	44	387	90	71	145	76	24	99	65
Salpae	1	6	0	0	0	0	0	0	0	0	1
Doliolidae	4	17	0	0	0	0	9	58	35	24	9
larv. Echinodermata	2	8	7	10	2	0	0	1	0	1	1
larv. Crustacea	7	13	14	37	62	43	30	31	10	11	4

where HT is the total entropy, HP (P stands for population) is that of species (or groups) joining the four samples of the same cruise, HS/P is the mean entropy of stations (S stands for station or space) weighted by the populations (species or groups), HS is the entropy of stations computed with the frequencies obtained with the total number of individuals per station, and HP/S is the mean population entropy weighted by the stations.

It is important to note, and to bear in mind in all that follows, that the two sets of entropies (one calculated from the specific composition of copepods and the other from the groups of zooplankton) are not completely comparable. In the first case, individuals of the same species can be considered interchangeable, but in the second, individuals of the same taxonomic group are not interchangeable. So, interpretation must be very cautious and must take into account the principle that has been used in the division of the set into separate items (MARGALEF, 1989). Diversity is a function of the organization of the ecosystem and is expressed and should be recognized at all levels of observation. In order to estimate the distribution of overall diversities, MARGALEF (1969b) recommended the use of a taxonomic group that covers a broad ecological spectrum, and not to use groups that are ecologically more specialized. In the marine environment, copepods are present throughout the year, and cover a wide spectrum of trophic positions. The measures of diversity made on the set of zooplanktonic groups has a different meaning as we shall stress later in the text.

If instead of considering the global system containing individuals and space as components we consider populations and space as two interacting systems, one of the SHANNON & WEAVER (1949) formulae allows us to compute the transmitted information between S and P

$$T(S,P) = HP - HP/S = HS - HS/P$$

where HP and HS are the information content of the output in each of the two interacting systems, and HP/S and HS/P are the corresponding ambiguity-functions, using the terminology of the theory of communication in a channel with noise.

We can compute redundancy or relative mutual information between space and population:

$$R = (Hmax - HT)/Hmax,$$

where Hmax = HP + HS.

RESULTS AND DISCUSSION

DISTURBANCES

In order to show the general evolution of the system and the moments when the main inputs of external energy took place, a synthesis of the hydrographic data (temperature, salinity, nutrients and chlorophyll) obtained during the sampled period is presented in figures 2-4. Two perturbations can be recognized in March and June. The first is typical at the end of winter, when the environment shifts from a high nutrient and well mixed situation to a more stable one, with growing incoming irradiance. In fact, the March sampling shows high and uniform salinity in the water column, but nutrients, although they are relatively high, have already dropped to one third of those found in December, while chlorophyll is more than 2 mg m^{-3}. So, the physical perturbation occurred before the March sampling, and phytoplankton had already reacted in March (response time of phytoplankton is of the order of 10 days or less). It is the phytoplankton bloom that must be considered to be the actual input of energy from the point of view of zooplankton.

The second disturbance occurred between the last sampling in May and that in June, and was due to an input of nutrients through the surface. It must be remembered that the stations are close to the coast (between depths of 20 and 50 m) and that they may be subjected to continental inputs as well as to perturbations coming from the shelf or the shelf break zones. In June, high levels of nutrients were detected at several stations. Some of them presented nutrient ratios characteristic of deep water (well compensated, from below the thermocline) while at least in one station, relatively high proportions of organic nitrogen and ammonia clearly showed a sewage outfall influence. Phytoplankton response to this perturbation is detected in the sampling of July, so that, from the point of view of zooplankton, the disturbance shows two aspects: a) an input of waters from different
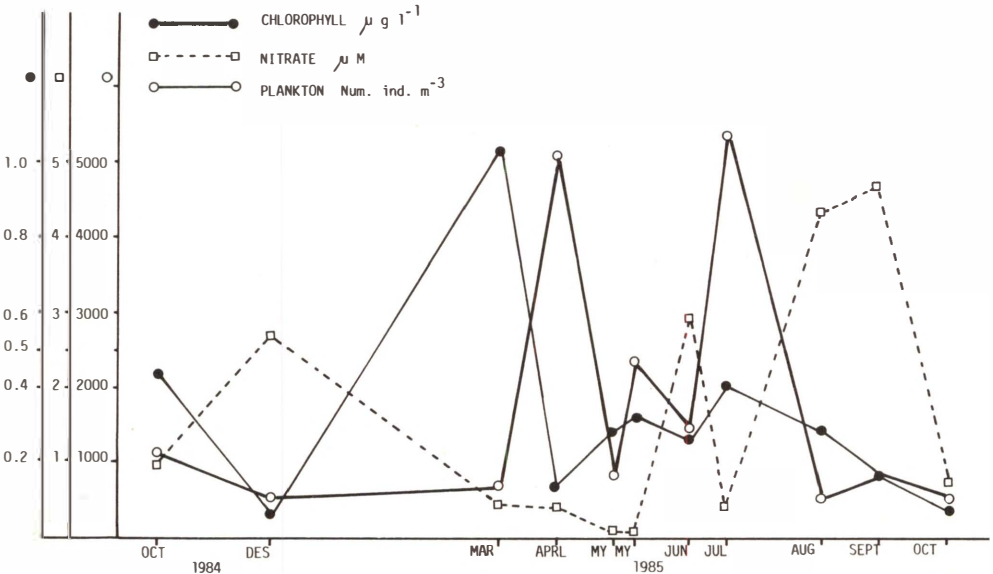

FIGURE 2. Mean values for the upper 20 m and the four stations studied of chlorophyll (μg l^{-1}) and nitrate (μM). Zooplankton is the mean value integrating from bottom to surface (20 or 50 m, depending on the station). Time of sampling is indicated on the horizontal axis.

sources in June with a general increase of nutrients, with an almost perfect vertical thermal homogeneity from the surface to at least 20 m depth; followed by b) an increase of exploitable phytoplanktonic biomass in July.

A maximum of nutrients was also observed in August, but it was followed neither by an increase of phytoplankton, nor by an increase of zooplanktonic biomass. So, this rise in nutrients cannot be considered a disturbance from the point of view of the plankton.

A first and simple approximation to the response of zooplankton to environmental disturbances is the distribution of the total number of individuals over time (Fig. 2). Copepods are always present during the annual cycle and their population most often accounts for 40 to 80 per cent of the total number of zooplanktonic organisms (Table II). However, they never exhibit numbers as high as those presented by cladocerans (maxima in April and July, when copepoda represent only 3 and 14 per cent of total organisms respectively). The higher numbers for total zooplankton are usually due to dense populations of cladocerans. In the first peak of zooplankton (Fig. 2), the density of cladocerans is very different from one station to another, while in the others they are more uniformly distributed in space. Other taxonomic groups contribute significantly to the relative maxima at the beginning of May. At the end of May the zooplankton is rather diverse, with cladocera, copepoda, siphonophora, appendicularia, medusae, pteropoda and chaetognatha larvae as main groups. In June, copepoda increase and cladocera decrease. In July, cladocera increase again, doliolids become important and chaetognatha increase. The disturbance of June was not uniform in space and neither was the response of plankton.

ZOOPLANKTON SUCCESSION

In what follows, it is important not to forget that entropy may be understood as uncertainty, so that a higher entropy means a more homogeneous set of frequencies. When entropy refers to populations (calculated on the frequencies of the different species or groups) high entropies
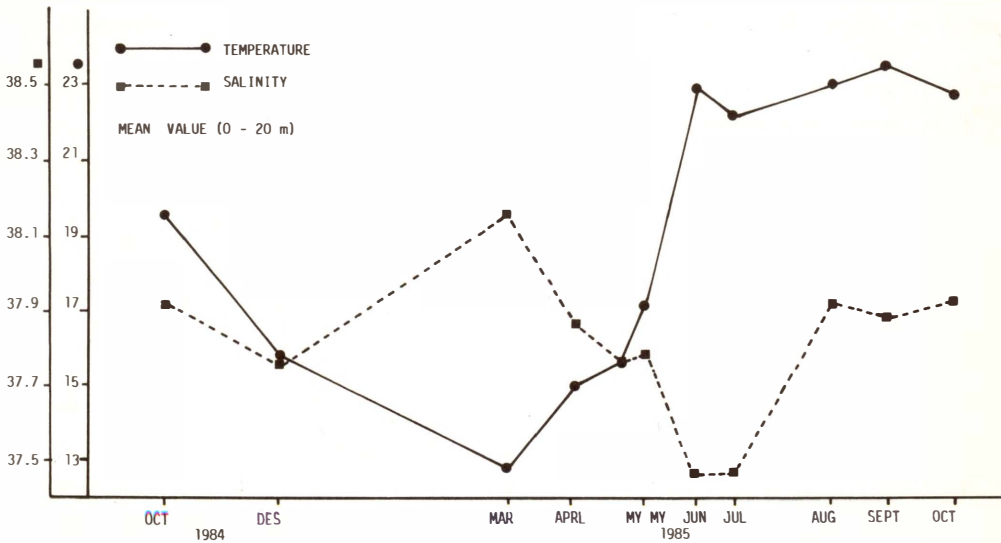

FIGURE 3. Temporal evolution of the mean values of temperature (^{o}C) and salinity for the upper 20 m and the four stations studied.

mean uniformity in the frequencies of species (high diversity) and low entropies mean that some species (or groups) are clearly more abundant than the rest. When the entropy refers to space (calculated on the stations, using the relative abundance of individuals in each station as frequency), high entropies mean uniformity in the total number of individuals per station, and low entropies mean that one or two of the stations present a much higher number of individuals than the others (there is heterogeneity among stations in terms of the total amount of individuals or biomass).

Absolute entropy values obtained for the populations of copepods are usually higher than those obtained for the zooplanktonic groups, because there are more species of copepoda than groups of zooplankton considered. On the other hand, there are always only four stations, so that the entropy of space is of the same order irrespective of the way in which the frequencies are calculated. In consequence, the relative contribution of space in the total entropy is higher when the groups of zooplankton are considered.

In figure 5 the evolution of total entropy is presented over a time span. The general trend is similar for both copepods and

groups of zooplankton, with some differences that will be discussed later. The first input of energy in March is reflected by the lowest total entropy. At that time, almost eighty percent of zooplanktonic individuals are copepods, but the total number of individuals is already rather low (less than 1,000 individuals per cubic meter, Table II). In April, cladocera increase in numbers and dominate the zooplankton, while copepoda decrease. Entropy of zooplanktonic groups remains low, but copepoda entropy increases a little. The highest entropy is reached in May, for both copepoda and groups of zooplankton. The second input of energy is also followed by an increase of cladocera (July) which is reflected by a low total entropy calculated for zooplankton groups, while the total maximum entropy is reached for both sets in August.

Maximum total entropy occurs in May and August, approximately two months after the inputs of energy. However, looking at the contribution of space in total entropy (Fig. 6) we realize that the absolute contribution when calculated for copepods rises from March to June, decreases in July and rises again during the summer. This means that the number of individuals for
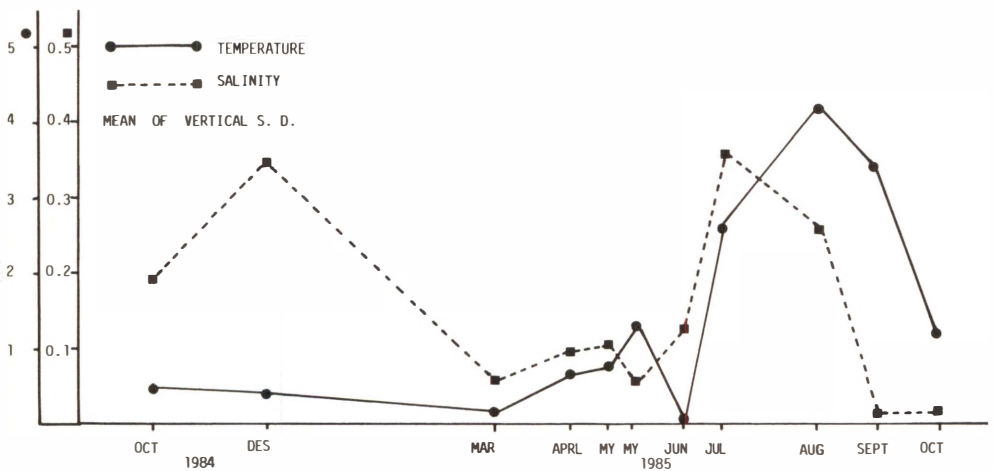

FIGURE 4. Temporal evolution of the mean value of the vertical standard deviation (in the upper 20 m) of temperature and salinity in the four stations studied.

the different species becomes relatively more uniform in space during succession. The entropy of stations calculated on the zooplankton groups has its minimum in April (when there is the maximum of cladocera) and rises in May, maintaining thereafter a similar absolute contribution until the end of the sampling period in October.

In terms of relative contribution, that is, the fraction of total entropy (HT) accounted for by HS/P, we realize that it is maximum, both for copepoda and zooplanktonic groups, in March, at the beginning of the successional process. The minimum is found at the time the total entropy is maximum (May and August), and rises at the end of the successional sequence. On the one hand, this U-shaped pattern follows approximately the inverse of the total entropy, which is logical because total entropy enters the calculations in the denominator (HS/P / HT). However, the mutual information between space and species (or zooplanktonic groups) gives us a clue to the interpretation (Fig. 7). Mutual

information (or redundancy in relative terms), is minimum at the time of the first input of energy for both copepods and zooplanktonic groups. For copepods, it rises to a maximum in the following sampling, to decrease steadily afterwards until the next input. For zooplanktonic groups, the rise is somewhat delayed, as is the second minimum after June.

In March, 6 species out of 22 account for more than 90% of the total number of copepoda, the same in every station. It seems that the input of energy represents a spatial equalization of biomass (high relative contribution of space) and a simplification of the composition of communities (low diversity). In April, the number of species of copepoda present in the samples decreases to 17 and only the biomass of a few species increases markedly in some spots, while the most abundant species present in March disappears from the scenario (because of decrease of relative contribution of space, increase of redundancy, diversity does not increase significantly). Once the first bloom
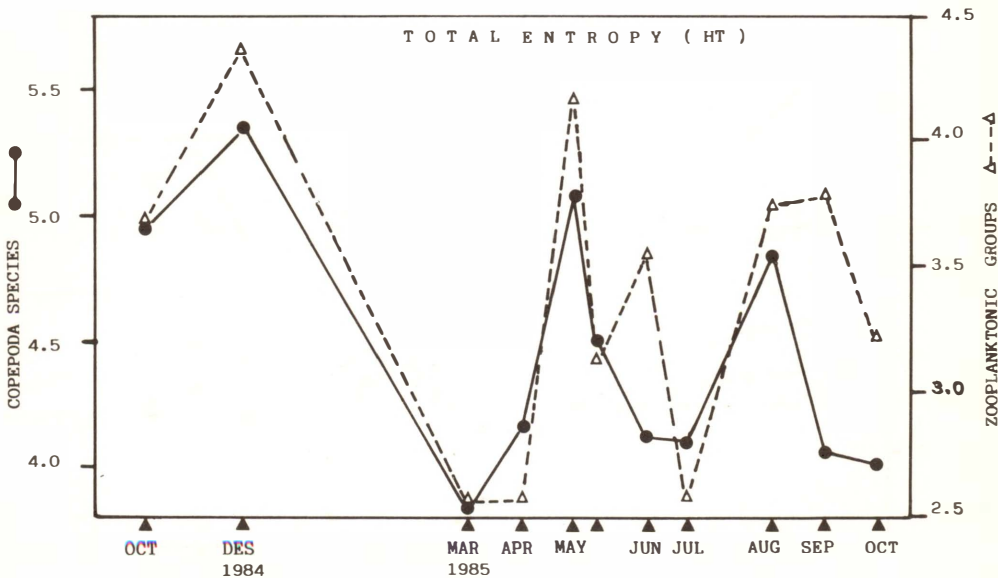

FIGURE 5. Temporal evolution of total entropy (HT) calculated for the population of copepoda and the groups of zooplankton.

of algal biomass has been incorporated in the trophic web, communities begin to organise, and the flux of energy per unit of standing biomass decreases considerably. The fact that in May chlorophyll is a little higher than in April, indicates that a flux of energy is maintained, helping the diversification of herbivores, but the presence of animals and presumably an increase of detritus and micro-heterotrophic organisms gives a more diverse environment from a trophic point of view (with a maximum of diversity for copepods and zooplanktonic groups in May and August). However, this moment of maximum specific diversity corresponds to a decreasing trend for redundancy in copepods and maximum redundancy in zooplankton groups. This moment corresponds to the minimum of relative contribution of space to total entropy and means that a maximum of specific diversification is reached, but without

uniformization in space. From this point, entropy is transferred to space, or in other words, spatial complexity reduces its grain, which is compatible with a reduced flux of energy and an increase of environmental physical stability. The decreasing trend in redundancy means a decrease in the degree of communication between space and species from the point of view of the biologist who is taking the samples. In fact, populations become more independent of space, and have the capacity to respond without great changes to the small disturbances occurring in an increasingly stable environment. The decrease in diversity with increasing stability in later successional stages was already pointed out by MARGALEF (1961).

In March and June we find the maximum concentrations of copepoda, and in April and July those of cladocera. The first response of zooplankton to each input of auxiliary energy ends with maximum
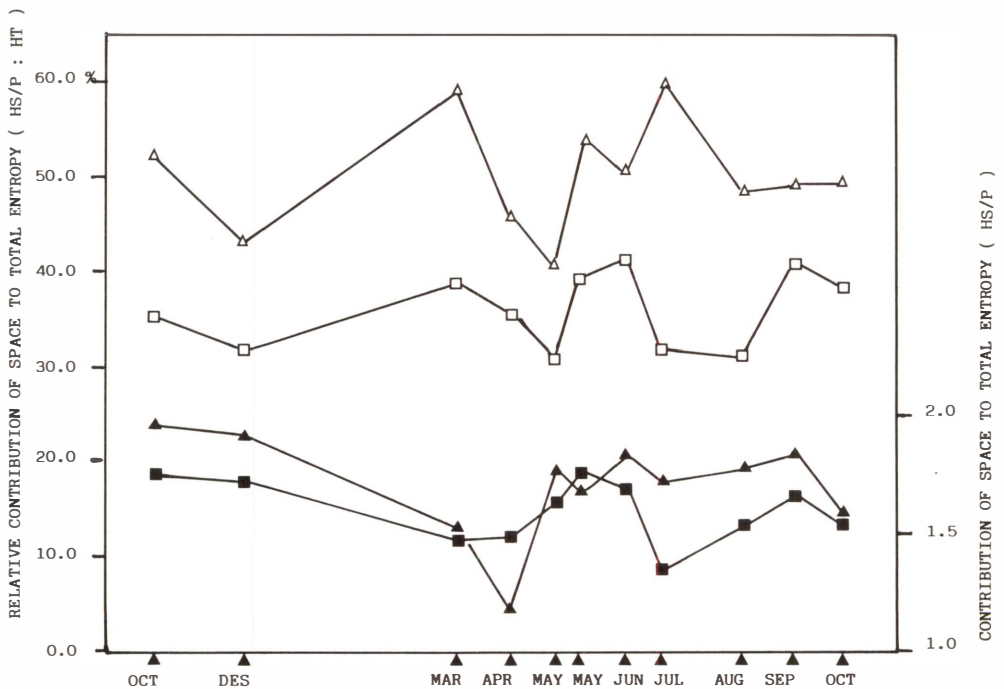

FIGURE 6. Absolute (right) and relative (left) contribution of space to total entropy for the population of copepoda (squares) and the groups of zooplankton (triangles).

diversity (in May and August). Changes of diversity are the outcome of the interference between mechanisms that regulate the numbers of species and those that are operative in relation to the total biomass or abundance. Diversity decreases when it is easier to add a species than to add an individual (MARGALEF, 1989). In other words, diversity drops when scarcity begins to play a role, and species are compelled to rework the biological matter that has entered the system. Then species become more connected. There are no means for populations to grow almost free from competition, and while energy is transferred to higher trophic levels, connectivity among species increases, bringing a concomitant decrease in diversity (MARGALEF & GUTIÉRREZ, 1983).

Comparing the total entropy measurements of the zooplankton groups and of copepods it may be seen that entropy of zooplankton groups remains relatively high while that of copepoda decreases (May-June, August-September). On the other hand, at least after the first input of energy, total entropy for zooplanktonic groups increases more slowly (or later) than the entropy for copepods. These facts, together with the delay presented by the maximum redundancy of zooplanktonic groups with respect to that of copepoda, indicates that succession proceeds in a hierarchical way (ALLEN & STARR, 1982; O'NEIL et al., 1986).

Finally, we computed the quotient between the diversity of species (or zooplanktonic groups) calculated from the sample obtained joining the eight samples from two consecutive cruises (the same four stations), and the mean of the diversities calculated for each sample. This quotient reflects the relative change of species (or zooplanktonic groups) with time. A quotient greater than one indicates change of species or groups, and of less
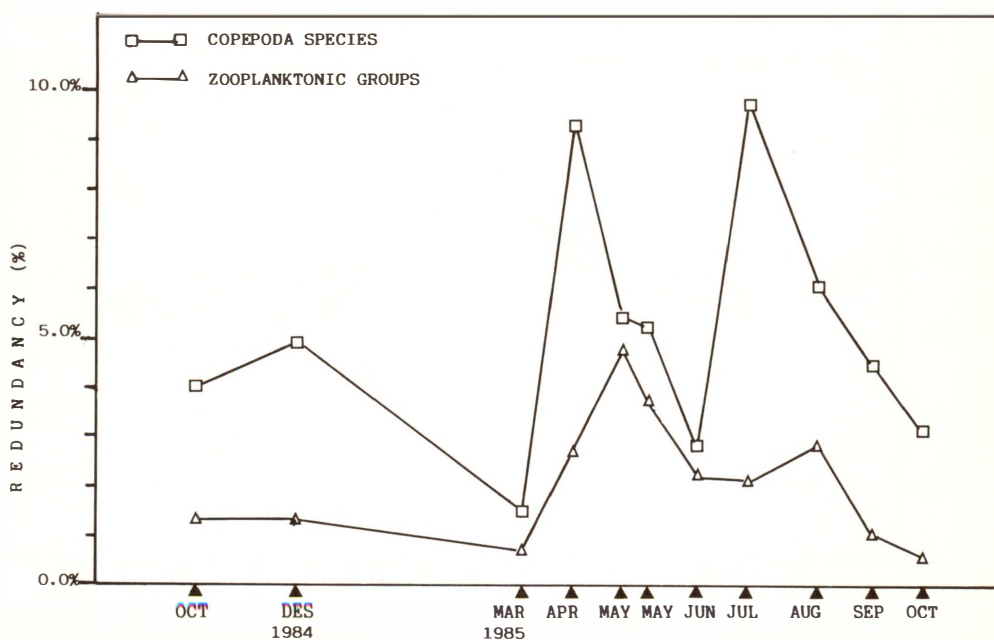

FIGURE 7. Relative mutual information (redundancy) between space and populations calculated for copepoda and for groups of zooplankton.

than one indicates a reinforcement of the present species or groups (Fig. 8). It can be observed that the greater change takes place between March and April, after the first input of energy, both for groups of zooplankton and for copepoda. Throughout the succession process, the specific composition of copepoda is changing, but with decreasing intensity, while zooplanktonic groups are reinforced between April and May.

At the end of the first successional sequence, zooplanktonic groups change again, but less than in March, and the rate of specific change of copepoda increases after the June input. From June to the end of summer, copepoda follow the same trend observed in spring, and zooplanktonic groups also show the reinforcement in mid-succession.

The unity of each successional event, which is initiated by a pulse of auxiliary energy, progresses in an increasingly stable environment and ends in another disturbance, is recognized by the trends of two parameters calculated from the populations of copepoda: redundancy (Fig. 7) and the rate of change of the specific composition (Fig. 8). However, measurements made on the groups of zooplankton allow us to recognize two parts in the successional event.

The first culminates with the maximum of copepod diversity (May and August), coinciding with the minimum contribution of space to total entropy, and reinforcement of zooplanktonic groups. The second part sees the diversity of copepoda decrease while zooplanktonic groups change and their diversity increases (June and September). Maxima of redundancy reflect the maximum of communication or matching between environment and populations. The initial increase of redundancy measured in the population of copepods (April and July) indicates this
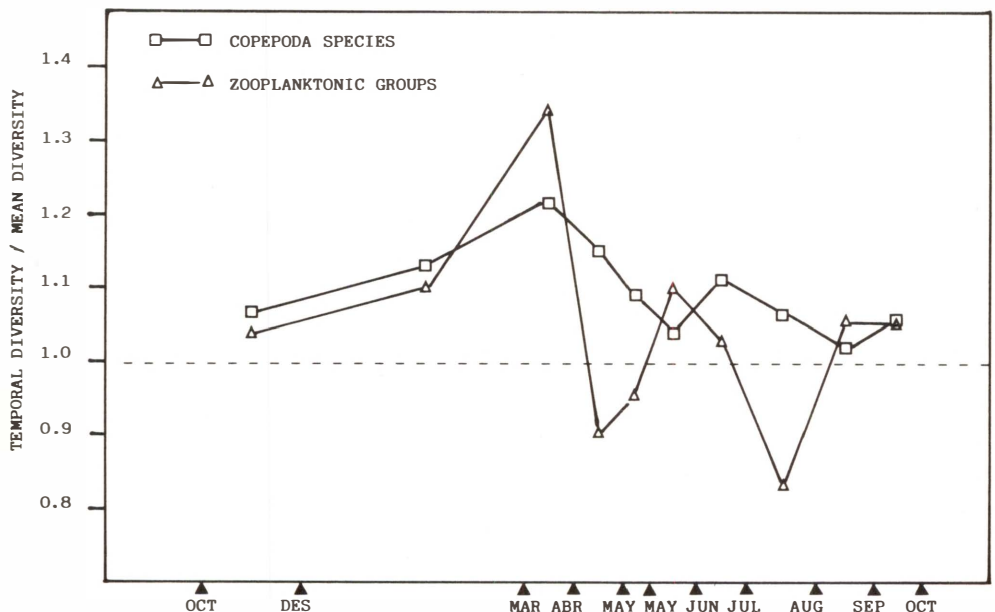

FIGURE 8. Quotient between the entropy of the sample obtained joining the two sets of four samples from successive cruises and the mean of the entropies of populations calculated from each one of the eight samples. The quotient was computed for copepoda and zooplanktonic groups. Values greater than one mean change and less than one mean reinforcement of previous biological composition. See text.

matching between chlorophyll and herbivores (represented in this case by copepoda), while the maximum of redundancy measured in the groups of zooplankton, indicates the matching of the first established populations that incorporated the input of energy, and the secondary populations that follow and feed on the organic matter accumulated in the environment.

The reinforcement of zooplanktonic groups, that is, their persistence over time, indicates their effective adaptation to the environment and accompanies their specific diversification (as is the case of copepoda). Once the initial fuel is consumed, a microbial food loop (POMEROY, 1974) develops and secondary phytoplankton communities emerge, which represent an environmental change to be coped with by zooplankton. The maximum redundancy of zooplanktonic groups indicates a match between what must then be considered the environment and zooplankton. Later, the rate of change of zooplanktonic groups increases. If the first steps in succession are governed by the degree of matching between temporal characteristics of physical phenomena and those of biotic responses (LEGENDRE & LE FÈVRE, 1989), in later stages, with increasing environmental physical stability, it is the biological composition and its chemical and physical implications that drive the system. Time lags appear between the first driving physical event and the resulting changes in pelagic food chains, but also between the first changes in pelagic communities and the following biological responses. We see here all the elements for a hierarchical organization of zooplankton during succession (O'NEIL et al., 1986).

These results are compatible with the increase of the mean size of organisms during succession (RODRÍGUEZ et al., 1987) as most bigger animals belong to some of the non-copepod groups. A shift in the mean size of organisms to larger forms must give a decrease of species diversity

measured within a taxonomic group (IGLESIAS, 1988), but diversity of groups can be maintained or even increased.

The trends observed give support to the idea that the communities selected or established in the first stages of succession, until diversity is maximum, become organized thereafter, increasing the number of effective connections in the food web, which is only possible if species diversity decreases. On the other hand, small disturbances occurring during the later stages of succession are assimilated by the populations. Their specific composition changes continuously though with decreasing rates, so that there is no equilibrium and we cannot speak of a persistent and steady state composition of species, although we may consider that this is the actual form of increasing stability in planktonic ecosystems. Manna models (WANGERSKY & WANGERSKY, 1980, 1983) predict that in stable conditions the total diversity can be constant but the species composition changes constantly.

We hold that the increase of spatial uniformity (mean entropy of space weighted by species) reflects the miniaturization of structure in very stable environments. Since our samples are integrated vertically through oblique hauls, we are dealing with horizontal spatial structuring. Patterns at scales of less than 1000 m, which are more closely linked to vertical structures, fall outside our observation window.

CONCLUSIONS

Zooplanktonic succession begins and is reset by inputs of energy. The two successional episodes observed in the present study are slightly different: the first disturbance represents a very large environmental change (vertical stabilization, increasing irradiance and temperature), so that many of the present species, adapted to a low flux of energy in

an unstable and cold medium, cannot persist. In terms of primary and secondary succession, this first input triggers what we could call a seasonal primary successional process in the neritic ecosystem. When the second input takes place, the environment is rich in biological types of zooplankton organisms, already adapted to high temperatures and vertical stability, and the microbial food loop is well developed. Response times are shorter and chlorophyll does not accumulate in the environment. During the summer inputs are not important enough to override the system that has been established in a physically stable environment, and the system adapts to disturbances without drastic changes of the biological composition of zooplankton. It must be said that the weather in October 1985 was much more a continuation of summer than the beginning of fall, so that we could not detect any interruption of the second successional process before our last sampling.

We conclude that decreasing mutual information reflects the internalization of environmental changes or disturbances. The shift from a physically driven system to a biologically governed one, although continuous, is marked by the maximum redundancy between space and zooplanktonic groups, and is reflected by a secondary increase in total entropy of zooplanktonic groups. During succession, there is no stabilization of the taxonomic composition, but a decreasing rate of its change, as well as miniaturization of spatial structuration. It is possible to look at these results as a case of a shift from a Lotka-Volterra to a manna type of community growth as conditions go from excess food evenly distributed to scarce food patchily distributed.

During succession, specific diversity measured on traditional samples (vertical or oblique hauls) reaches its maximum halfway through the process, while there is still a high enough externally driven flux of energy to allow a reduced degree of inter and intra-specific interactions. The accumulation of matter in life-forms reduces the energy flux per unit of biomass and brings scarcity into play. The reworking of matter forces the increase of connectivity among species and the decrease of specific diversity. One of the effects of this would be a hierarchical shift of control to those species in plankton with a broader activity range (bigger, with a higher motility). These species would help the spatial organization of plankton and lengthen the trophic or behavioral paths connecting species. This would represent a decrease of connectivity as some potential relations could be cut, so that a hierarchy or "chain of command" structure (MARGA-LEF, 1989) could develop.

Further research is needed to elucidate whether there is actually a shift in the scale of spatial structuring in the system (miniaturization) that might help to relieve effective connections among species in a higher order spatial scale, which could preserve a relatively high overall specific diversity; this diversity would otherwise be much lower.

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