4.63 SUCCESSIONS OF POPULATIONS

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4.631 INTRODUCTORY STATEMENTS

Mixed populations or biotic communities in a steady state are the exception in nature. Commonly there is a continuous shift in their structure, steadily adjusting itself to a changing environment. Even populations living in a relatively constant environment or in an environment that changes only by reaction of the community, experience a continuous reorganization.

In ~~such~~ the general case, the composition of the mixed populations in successive times, reflects the historic nature of biotic communities. Change is not haphazard, but progressive or directional, like matura~~tion~~ing and aging of an organism ~~and~~ or evolution of a species. It is a fortunate property, since it enables a certain amount of prediction about future changes. Theoretically, an accurate prediction would need the complete analysis of elementary relations and feedback circuits in an ecosystem. Regularities induced from empirical and comparative stud~~y~~ies of successions allow ~~to~~ the bypass~~ing~~ing of such needs ~~in a certain sense, when~~ in cases where a not too ~~concrete~~ detailed forecast is desired.

All of the dynamics of communities involved in the directional change towards a ~~[illegible]~~ rarely attained stable state should fall unto the heading of succession. The idea of succession was born in terrestrial plant ecology, but its usefulness has been proved in other fields of general ecology.

Succession is related to environment. By the process of succession, the ~~ecosystem~~ community becomes more precisely adjusted to environment. As a criterium of adjustement we feel inclined to consider the maintenance of the maximum total biomass with minimum relative energy dissipation or minimum rate of increase of entropy (minimum relative entropy production by the ecosystem). This is an anticipation of a conclusion to be reached later. Equilibrium conditions within the ecosystem become more important than variations in inputs and outputs, and the conditions of stability of an open system is approached. If ~~it~~ this is so, the driving forces in succession are internal to the living structure of the ecosystem, They regulate numbers in species and accept or reject new potential associates introduced at random, under the controlling action of environment, striving always to an increase of the efficiency.

On the other hand, a theoretical image of succession can be constructed deductively on the basis of the properties of organisms and of populations. In this way, the accepted principles of populations dynamics and selection, allow ~~to~~ forecasting a certain trend in the evolution of ecosystems, and the fulfilment of such a trend is the empirically etablished succession.

The terminal stage of a succession, where the ecosystem has reached full equilibrium with external abiotic factors and with the existing supply of accessible species, is called the <u>climax</u>. We can dispense with this highly controversial and speculative concept. Instead we should refer simply to the relative position of different ecosystems along a succession, calling them more or less <u>mature</u>. Maximum possible maturity would be reached at the climax. The relative degree of maturity can be assessed through many independent criteria ~~and are~~ that do not imply the recognition of ~~not necessary to recognize~~ the exact position of the ecosystem in a definite point of an actual succession.

A distinction is traditionally drawn between <u>primary succession</u>, the development of an ecosystem in a new biotope, with etablish~~e~~ment of a new pattern, something r~~i~~essembling morphogenesis in an organism, and secondary succession or reconstruction of part of an ecosystem that has been disturbed or ~~whipped away~~ removed by some external agency, and that r~~i~~essembles more regulation or regeneration in an organism. Secondary successions are always on the way, as patches of less mature character in an otherwise ~~more~~ homogeneous ecosystem. Accumulation of dead material, of excrements, of corpeses, is followed by secondary successions of lesser entity, that can be called micro-successions and that also become integrated in the general succession. Primary and secondary successions may be considered together as forming the ontogeny of the climax. Then, it is possible to speak of the phylogeny of the climax, ~~meaning~~ the accretion of new successional stages through evolution of species along time.

The succession may ~~be~~ show discontinuities or relays (Dansereau, 1954), when the controlling agents change. ~~and~~ This leads to a different exploitation of the resources. Relays are often a consequence of the reaction of the community upon the environment. Ex~~e~~amples: benthic successions are controlled firstly by the nature of substratum and later by the intensity of light; accumulation of sediment near the shore brings the ecosystem out of water, ~~such~~ leading to utilization of atmospheric CO_2.

The process of succession can be appraised separately in different levels or in different local structures of the ecosystem. Succession runs with a different speed and with different characteristics in the different trophic levels or even in the different niches of an ecosystem. In a given ecosystem, higher trophic levels have always a more mature character. Changes that at the inferior levels -say, in the phytoplankton- retain all the dynamic notes of a true succession, become integrated in the whole ecosystem with changes in other trophic levels -grazers, carnivorous zooplankton- that have the character of small <u>fluctuations</u> of populations or even of <u>internal</u> <u>rhythms</u>. Length of life or generation time in individual organisms, as related to length of period of environmental changes is an useful criterium for judging on the impositions of the environmental changes upon the ecological niche, and Birch (1960) has ~~[illegible]~~ stressed the importance of this relation also from a genetic viewpoint. Organisms with a long life smooth changes of successional nature and contribute to the general stability of ecosystem.

Every environment subjected to strong fluctuations or periodic changes of a catastrophic nature, allows succession to proceed only up to a certain point, to be abruptly cut here and begin anew. Of course, superior trophic levels can remain less perturbed than the producers' level, but anyhow cannot attain a high degree of maturity. In ~~such~~ these cases, we are faced with open systems with ~~so~~ such great changes in input and output, that internal conditions of equilibrium are unable to lead to a steady state. In a general way, as Dunbar(1959) puts it, oscillation of the properties of environment in higher latitudes makes impossible stability of ecosystems; on the contrary, ecosystems are often highly mature and specialized closer to the Equator. Fluctuations are reflected both in the community and in the environment, that is, in the whole ecosystem.

After careful comparative study of empirical evidence on successions, it is possible to isolate a certain number of operations common to all successions, that allow ~~to~~ the recogni~~se~~tion of the relative maturity of the sampled ecosystems under comparison, without the necessity of stating a before-after relation between them, along a common line of succession. In fact, terrestrial ecologists describe also the successions very often without actual evidence, based only in the operation of principles that they have intuitively recognized, in relation to a certain geographical pattern.

If degree of maturity can be assessed in an independent way, the criteria adopted to define it may be useful for classing communities and ecosystems, ~~if the need is felt for such a classification.~~ As in taxonomic procedure, phylogenetic criteria are the best, there seems to be little doubt that successional or maturity criteria have ma~~y~~ny advantages for the classing of ecosystems, allowing ~~to~~ a generali~~ze~~tion ~~to~~ for a whole class of certain dynamic properties of mixed populations.

4.632 SELECTED EXAMPLES OF MARINE SUCCESSIONS

~~Some actual examples of marine successions may provide a factual basis for a later discussion of the general principles of succession.~~

i. Experimental surfaces. Fouling.- On a solid surface, newly exposed, succession begins with the formation of a slimy film, with bacteria and diatoms. These organisms increase rapidly. After a few days, protozoans develop in growing numbers and cause a reduction in the density of bacteria populations. Larvae of barnacles, endowed with a great facility ~~p~~ of dispersal and produced in enormous numbers, develop ~~also~~ rather soon; intensity of barnacle fixation ~~is~~ shows a seasonal dependen~~t~~ce. ~~of season; anyway~~s, The attachement of barnacles is favoured by the presence of the slimy film of organisms previously developed. Alternative or superposed paths of succession are the development of hydroids and ectocarpaceae. This stage is realized in about one or two months after start of succession.

Occupation by bryozoa, encrusting algae, eventually by Ulva, is slower, but ~~safer~~ more secure, and leads to a more structured community, encroaching over the previously developed organisms. Ulterior succession is strongly bound to the supporting capacity of water bathing the surface. After the first protozoa, develop catchers (Hydrozoa, cirripedia) and in later stages filter feeders can assume the maximum development (sponges, tunicata and mussels). Sponges behave as very invasive animals, but mussels and oysters are more able to stand fluctuations in the level of sea and thrive unenhanced in the superior belts. The community is, thus, becoming heterogenous, zonate, when one year or more is elapsed.

The preced~~ent~~ing description fits well to succession on ships, buoys, submerged experimental panels and roots of mangrove (Aleem, 1957;

Coe & Allen, 1937; (Hoshiai, 1956; Huvé, 1953; Redfield & Deevey, 1952; Sheer, 1945; Skerman, 1956). As succession proceeds, the community becomes more complex, with more ecological niches; parasites and symbionts are increasingly represented; and the surface colonized by animals in relation to the surface colonized by algae increases. In the firsts stages, texture and nature of substrate may be decisive, later orientation becomes important, but even this factor may be minimized by encrusting organisms. A new type of heterogeneity develops, in relation to distance from level ~~of~~ sea and, in part, to orientation.

The ~~dominant~~ plant organisms that become successively dominant, as bacteria, diatoms and macroscopic algae, increase in ~~individual size~~ number during ~~along~~ succession, but their rate of increase drops. Animals ~~proper of~~ belonging to the first~~s~~ stages are endowed with enormous powers of dispersal and rapid growth. Forms developing later grow slower. Possibility of getting food from plankton is ~~material in the~~ a determinant~~ion~~ ~~of~~ in the final stages of succession. Forms developing later in the succession, in general, are not so able as those in the firsts stages to resist fluctuations in level, light and food.

ii. Other benthic communities.— Many of the successions described in natural benthic communities are ~~rather~~ reconstruct~~ions~~ed ~~based~~ on incidental or indirect evidence and often on theoretical considerations. Notwithstanding, some descriptions, refering chiefly to littoral algae, are based on actual evidence (Hatton, 1938; Moore, 1939; Southward, 1953, 1956; Varma, 1959). ~~Here~~ We ~~want just to~~ single out ~~a couple of~~ several examples ~~apt to~~ illustrate ~~the~~ ~~some~~ of some ~~[illegible]~~ general principles. ~~they help to illustrate.~~

Proximity of shore is important ~~as related~~ to the stability of the environment. According to Shelford & al. (1935) the community of *Balanus*-

-*Littorina* develops in a few months. Such a short time may imply that succession does not proceed very far, and this agrees with its development in an environment subjected to fluctuations (rocky shore). The succession leading to the *Strongylocentrotus-Argobuccinum* community is slower or lasts for a longer time, since a bottom of shell has to be built over the substrate of mud or sand, before reaching a ~~notable~~ stability~~, of ecological conditions~~.

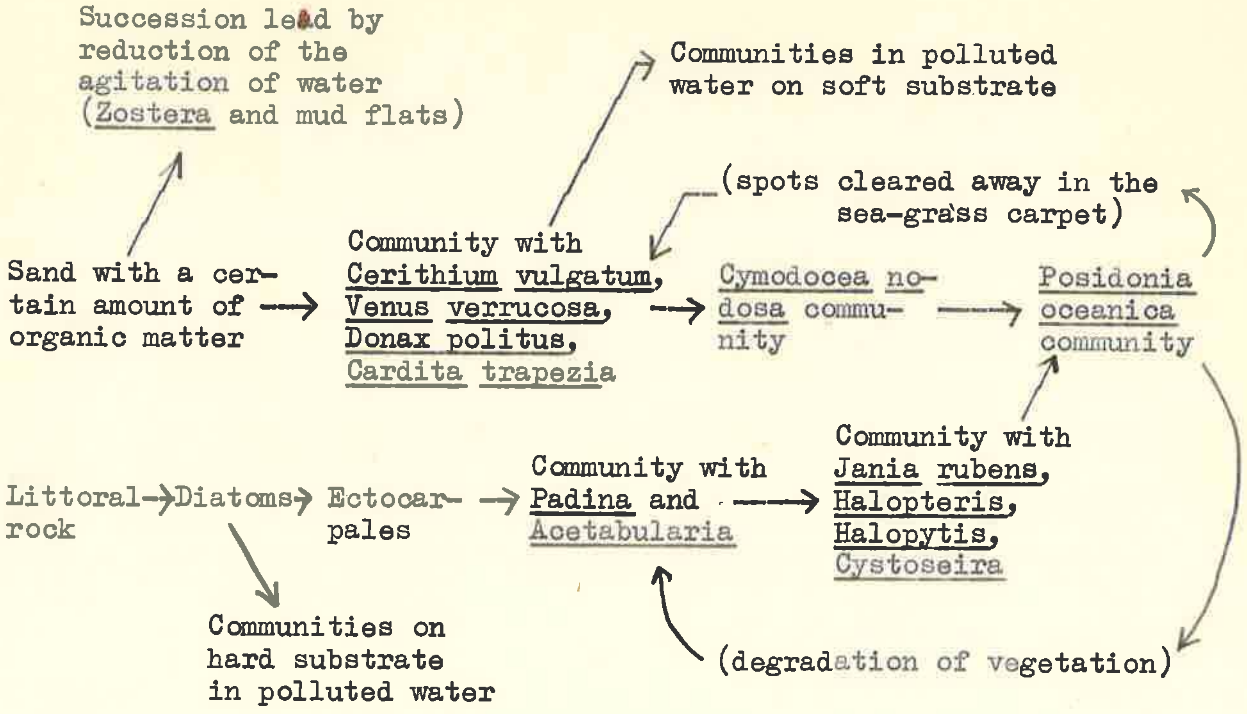
Zones of vegetation around a senescent lake represent, obviously, stages of a progressing succession ~~going ahead~~. Speculation on translating zonation into succession can be reliable ~~sound also~~ in some marine communities, especially in littoral ones on soft bottom, such as sea-grass meadows, mangrove, and perhaps in some forms of coral reefs. But zonation in communities over hard or stony substrata, on erosion coasts, has nothing to do with succession and represents simply an advanced stage of the adjustment of communities to a substrate. ~~that~~ ~~This substrate is~~ ~~If subjected to change, this is in the sense of being perpetually renewed, and remains steadily like itself.~~

Den Hartog (1959) describes how ~~accepts the development of~~ zonation develops along the succession of the vegetation in the coasts of the southern North Sea. In the firsts stages, most of the eulittoral region is occupied by the *Enteromorpha compressa*- *Porphyra* community . Later the vegetation becomes heterogenous, segregating a lower belt of the *Polysiphonia-Chaetomorpha* community , a superior belt of the *Fucus vesiculosus* community and a medium zone belonging to the *Cladophora* formation. The last, as succession proceeds further, splits into different belts characterized, up to down, by *Fucus vesiculosus*, *Ascophyllum* and *Fucus serratus* respectively.

iii. The formation of sea-grasses.- A considerable amount of work has been devoted to the study of developmental stages in sea-grass communities (Aleem, 1955; Hatton, 1938; Molinier & Picard, 1952, 1953, 1954; Pérès & Picard, 1955, 1958). Sea-grasses require an intense illumination and, in general, develop not deeper than 10 m. Sea-grasses make easy the accumulation of sediments, where their rhizomes stick, growing continuously towards the surface.

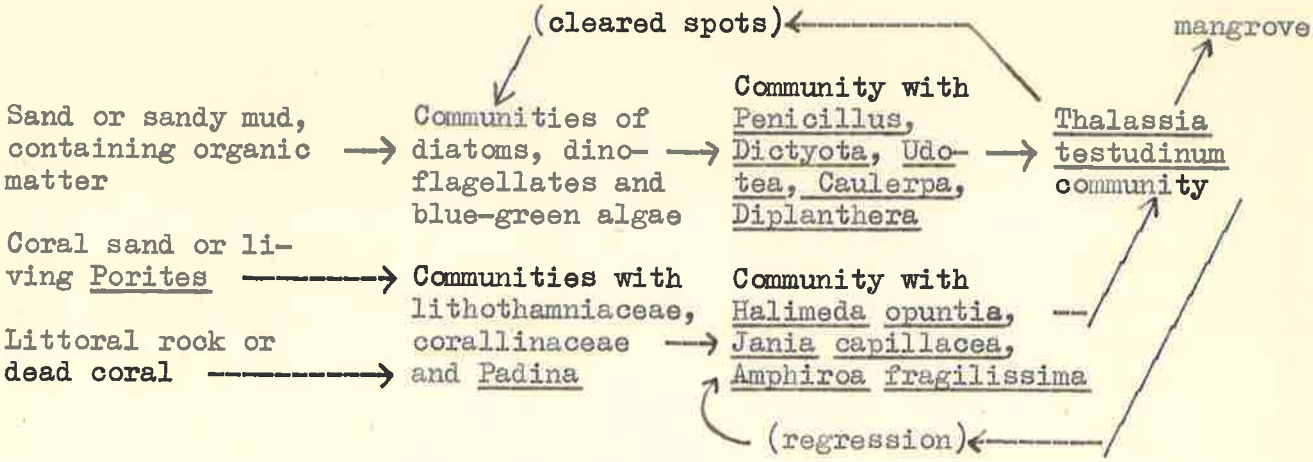
If growth is unchecked, when the community near ~~the~~ sea level, new ecological conditions are established, not reconciliable with the persistence ~~existence~~ of the same type of vegetation ~~plant association~~. It is a point for a relay, not accomplished, in the Mediterranean shores, but clearly represented along the tropical coasts by the invasion of mangrove, of Rhizophora mangle. The shade of mangrove is detrimental to the sea grasses ~~(for instance, to Thalassia)~~ and silting between the advancing roots of mangrove, after elimination of the grass, establishes the appropiate conditions for the implantation and growth of the viviparous fruit. The mangrove belt progresses towards the sea, and on the side of land, new stages of terrestrial vegetation develop. Alternatively, extensive mud flats, often controlled by fiddler crabs, may be considered as a sort of detention or regression of the succession.

Sea-grass communities can colonize different types of substrata; initial composition of the respective communities may be different, but the different seres converge later in the time. In the Mediterranean, the Posidonia community is considered by Molinier and Picard as a climax: most of the areas able to support it are already in such a terminal stage. On the basis of the research done by Molinier, Pérès and Picard, succession in the Mediterranean can be summarized as follows. ~~Pérès and Picard (1958) report a great deal of information relative to the rich, and often characteristic fauna, of the several stages.~~



Growth of Posidonia gives origin to a sort of reef, with a back lagoon of calmer water, where thrive Cymodocea, Caulerpa and other plants. Advanced stages in succession are more sensitive than pioneer stages to the effect of environmental changes. When subjected to a stronger and unusual turbulence, ~~e.g.~~, the development of the Padina-Acetabularia community would slow down, and that of the Jania community would stop completely, Cymodocea did not develop and Posidonia, the most sensitive would die. Advancement of succession requires, then, a certain stability in environment and, as always, pioneer stages are more resistent to fluctuations in ecological factors.

A proof of the soundness of this general scheme of succession is the fact that a parallel plan can be drawn for the Thalassia community in tropical waters, e.g. in the coasts of Puerto Rico (Margalef & Rivero, unpublished):



<u>Halimeda</u> and the corallinaceae are very effective builders of sediment, owing to the calcified nature of the discarded pieces of the thallus.

Similarities with the Mediterranean communities extend to many others details of structure and development of vegetation, not included in preceding sketches. The counterpart of the Antillan community with <u>Penicillus capitatus</u> and <u>Diplanthera wrightii</u> has been described by Gilet (1954) in the Mediterranean and includes <u>Penicillus mediterraneus</u>, <u>Caulerpa olivieri</u> and <u>Zostera</u>. It is easy to discover other parallels in the animal life: Picard and Molinier compare the presence of the foraminifera <u>Orbitolites complanatus</u> on the leaves of <u>Thalassia</u> with the presence of a fixed variety of <u>Sorites variabilis</u> on the leaves of Mediterranean <u>Cymodocea</u>.

<u>iv. Coral reefs and coral-like formations</u>.- Hermatypic ~~[illegible]~~ or reef forming} corals are the basis of very mature ecosystems and, as a matter of fact, develop only where stability of environment is great. In temperate and cold latitudes, fluctuations along the year are too important to allow reefs to develop. One can speculate that the consortium coelenterates plus zooxanthellae ~~need~~ ~~exiges~~ require relatively stable environmental conditions and that perhaps ~~[illegible]~~ this condition of stability more than

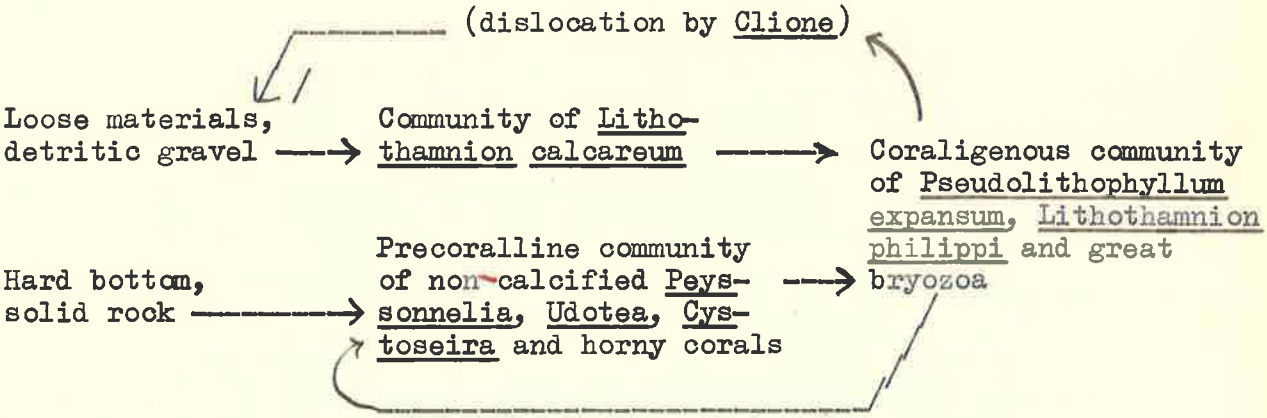
temperature is the actual limiting factor in the geographical distribution of hermatypic corals. Developing further the same line of thought, we may suppose that a periodical enrichment in nutrients would result in yearly pulses in the growth of the "captive vegetation", and perhaps such a condition cannot be harmonized with a steadily growth of polyps and exploitation of the algae. It has been observed ~~(unpublished)~~ how in conditions of ~~plenty~~ an abundance of nutrients, the algae overgrow~~th~~ the polyps of Porites, ~~[illegible]~~ leading them to a ~~bad~~ degenerate condition.

Coral reefs are incessantly subjected to destructive and reconstructive processes. Secondary successions lead denudated parts to a structure similar to the mature coral reef. ~~In~~ The ~~bulky~~ extensive literature on coral reefs contains many examples of ~~many data are to be found relative to~~ the secondary successions. ~~in the reef, and other evidence supporting the belief that coral reefs are perhaps the more mature type of ecosystem living recently in the seas.~~

The terminal phase in the growth of a reef seems to be controlled by competition for light (Gravier, 1910). Species that grow fast, building expanded and foliaceous surfaces, are at advantage, except when and where the sea is too rough and breaks the colonies. The orientation of surfaces in relation to light (and also to flow of nutrients ?) has a lesser importance in deeper water, where light is not so strongly directional. Only one exemple will be reported here: Acropora palmata, with broad, elk-antler-like, ramifications, is a madrepore that frequently is ~~the~~ dominant from the surface of the sea to 6 m depth in the Caribbean reefs (Goreau, 1959). It ~~seems~~ appears that proliferation of this species indicates a later stage in the development of the reef community. Acropora pushes over a basement of other species (Montastrea annularis in Jamaica) and grows rapidly on the crest of the reef (Vaughan, 1951). Quantity and composition of the pigments of its zooxanthellae ~~[illegible]~~ compare with those of a phytoplankton of great activity (Margalef, 1959). But Acropora palmata is fragile and easily torn out; the surface of denudated coral rock is soon covered by zoanthidea (Zoanthus sociatus, Palithoa caribaea) and other pioneers of secondary successions.

In temperate seas, at a depth where the environment is relatively stable, communities develop that offer many similarities with the rock building corals, ~~as~~ They contribute also to the ~~concrescence~~ cementation and fixation of loose materials into ever bigger and more stable masses, leading to a community of relatively slow turnover, where encrusting organisms predominate or are the dominants.

In the Mediterranean, such precoraligenous or coraligenous communities develop on ~~little perturbed substrata~~ quiet places, with small afflux of detritic material coming from shore and areas of rather low illumination. Pérès & Picard (1958) summarize succession under such conditions as follows:



The precoralline communities have a partial resemblance ~~with~~ to the communities ~~on~~ hard substrate which ~~that~~ precede the sea-grass terminal community. the ulterior path taken by succession, if towards coralligenous communities or, instead, towards sea-grass meadows, seems to be a ~~matter~~ function of the amount of light received and of the influx of finely divided detritic material.

In tropical and warm temperate seas with tides of low or negligible amplitude, a fringe or cornice of encrusting red algae develops on the rocky shores, close to the sea level. It exemplifies many dynamic aspects of succession. Development of the dominant species (in the Mediterranean "trottoir", <u>Lithophyllum</u> <u>tortuosum</u>) leads to a diversification of biotopes (shadowy places beneath, small hides in the mass of the "reef", etc.). In the final stages, animals of terrestrial origin are often found, ~~more or less adjusted to the special conditions encountered here~~.

<u>v. Plankton</u>.- The study of development of plankton is ~~made complex~~ complicated by the fact that <u>sequence</u> of populations, as recorded in a geographically fixed point, is the result of a combination of <u>succession</u> and <u>traslation</u> ~~or transport~~ of water masses. A considerable knowledge of hydrographic conditions is required to reconstruct true succession.

Environment is periodically changed one or more times in the year, at least in cold and temperate seas, through increase of turbulent mixing and enrichment of nutrients. The sequence of communities that starts in the homogeneized condition of turbulent water and proceeds as stabilization of the water mass increases, nutrients are consumed and miscellaneous ~~metabolites~~ (?) organic substances excreted into the water, has many characters of a true succession in a stable environment. Succession in plankton shows no important relays and when it is possible to discover ~~well defined~~ clear cut limits between stages or "periods" characterized by biotic composition, they are generally due to the traslation of water masses.

Plankton ecosystems ~~are very~~ ~~provides~~ are highly productive (~~[illegible]~~ "autotroph", as Odum calls the ecosystems where quotient between total production and total respiration ~~[illegible]~~ exceeds unity), ~~and~~ Their excess of production, that in part goes to benthic communities, is ~~implies~~ coupled to a notable speed in succession. It can safely be concluded that pelagic ecosystems never

exceeds

attain a high degree of maturity or retain ~~with~~ lower stabilities in ~~much less due to it~~ the inferior trophic levels (phytoplankton). Even stabilized water experiences a loss of plankton by sedimentation. ~~and a certain input of new nutrients.~~ Pelagic communities never attain a state comparable to the climax of terrestrial or benthic populations.

~~Succession results from the play of environmental factors and factors intrinsec to the population. Simple regression of population composition against environmental factors cannot give definitive clues for explaining changes in populations. One has to count always with an "historic contamination".~~

There is an inmense literature dealing with cycles of plankton in different ~~seas~~ marine areas. Experimental approaches in culture vessels and tubes could contribute very important data, but so far ~~no much~~ little useful work has been carried ~~on for the understanding of~~ out with regard to the mechanism of succession in complex ecosystems. ~~When we want to extract a~~ Attemps to obtain summar~~y~~ies of general application, ~~we~~ are ~~confronted~~ hindered ~~with~~ by what ~~it~~ seems at first confusing evidence. ~~But if~~ We can, however, restrict ourselves to ~~single out~~ a few broad non-contradictory statements, ~~it is possible to avoid too much contradiction.~~

Phytoplankton.- In a general way it can be stated that development of dinoflagellates follows development of diatoms, and that zooplankton increases with a certain time lag in relation to phytoplankton. For descriptive and reference purposes we want to distinguish three stages in phytoplankton succession.

A number of species are consistently recorded as part of the flowerings initiating succession: Chaetoceros debilis, Thalassiosira antarctica, Th. gravida, Th. nordenskioeldi in very cold water (1 to 5 ºC), and, in less extreme thermic conditions: ~~Chaetoceros~~ Bacillaria paradoxa, Chaetoceros *affinis*, *Ch. compressus*, *Ch. radians*, *Ch. socialis*, *Ch. tortissimus*, *Distephanus speculum*, *Exuviaella baltica*, *Fragilaria antarctica*, *F. nana*, *Leptocylindrus danicus*, *Nitzschia delicatissima*, *Porosira glacialis*, *Skeletonema costatum*, *Thalassionema nitzschioides*, and ~~[illegible]~~ many small flagellates. Less characteristic are *Chaetoceros densus*, *Guinardia flaccida*, *Rhizosolenia stolterfothi*, *Thalassiothrix frauenfeldii*.

The second stage is characterized by the development of the bulk of diatoms, including most of the planktonic species ~~of such group belonging here,~~ and a certain number of dinoflagellates, as *Ceratium furca*, *C. fusus*, *C. tripos*, *Peridinium brochi*, *P. trochoideum*, *Prorocentrum micans*. Towards the end of this stage are common *Bacteriastrum*, *Corethron*, *Nitzschia delicatissima*, *N. seriata*, *Rhizosolenia alata*, *Rh. calcaràvis*, *Rh. hebetata*, *Rh. imbricata*.

The diatoms of the third or terminal stage of succession are few, e.g., *Hemiaulus hauckii* and some *Chaetoceros* associated with tintinnids. Dinoflagellates are represented by ~~plenty of~~ many forms of the genera *Ceratium*, *Dinophysis*, *Goniaulax*, *Ornithocercus* and others. Coccolithophorids with elaborate calcareous shells are also present. If succession does n end ~~as~~ [illegible] here ~~out~~, ~~towards the in the~~ further stages are characterized by a number of ~~[illegible]~~ species with reduced chromatophores and often bizarre form: *Ceratocorys*, *Histioneis*, *Ornithocercus*, *Oxytoxum*, *Podolampas*, *Pyrophacus*. If succession can continue without a reduction of nutrients supply, the terminal stages are represented by a heavy accumulation of dinoflagellates, in patches near the surface, as a "red tide". Red tides belong always to a final phase of succession, being preceded in general by diatom blooms.

In freshwater lakes a pattern of succession is encountered whose parallelism to the succession in marine phytoplankton can be adscribed to the operation of ~~the same~~ similar causes. In the first stage, with actual vertical mixing, *Melosira* species can be found. Then develop chrysophyceae and different diatoms, as *Asterionella formosa*, *Fragilaria crotonensis*, *Tabellaria fenestrata*. Characteristic of the later stages are organisms floating through gas or fat vacuoles , as *Anabaena*, *Aphanizomenon*, *Botryococcus* and *Microcystis*, or by organisms with their ~~its~~ own swimming powers, as *Ceratium hirundinella*.

Zooplankton.- Animals have a ~~live~~ longer life expectancy than plants and their populations are based on more complex relations. It is hardly possible to reach any ~~say anything~~ generalizations on zooplankton succession.

Development of copepods follow the peak of phytoplankton production with a time lag of about two to three months. In some favourable situations it has been possible to follow an initial ~~a first~~ development of species feeding on small algae, as *Oithona*, being followed by *Calanus*, *Temora*, and, finally, by the adults of predatory copepods.

In the Mediterranean, tintinnids with a weighty lorica (*Stenosomella* and others) develop with the first stage of phytoplanktonic succession, in coincidence with actual upwelling or convective movement of water. Characteristic of terminal stages are true pelagic forms with a light lorica, as *Eutintinnus* or *Favella*.

Distribution of successions in the year.- Very commonly two successions of unequal lenght start every year. The succession starting in winter or spring and lasting up to the end of summer is the longer. Then, another succession is started in fall, but it does not proceed very far, and soon is relayed by the new succession of next year.

Even summer successions in the temperate-cold and cold seas are commonly interrupted after arriving to a stage similar to our second. But in the Mediterranean and, in general, in the warmer seas, a much more complete picture is observed. Here the third stage with an increasing representation of heterotrophic forms is very well developed and lasts ~~a long time~~ for many weeks and even months. Therefore, it can be said that the pelagic ecosystems attain in the Mediterranean a higher degree of maturity than in the Northern Atlantic.

Thermic cycles cannot be decisive in the determination of the planktonic successions, since a similar pattern is observed under very different temperatures: in the range from 3 to 16ºC along the Northern coasts of Europe and America, and between 13 and 27ºC in the Mediterranean. ~~Other~~ Simil evidence ~~in the same sense~~ comes from the fact that in appropiate places, as in the bay of Vigo (NW Spain, Margalef, 1958), not one, but 3 or 4 complete successions are counted in the course of a year, and all of them start with species that ~~[illegible]~~ in the literature have been considered as "spring" or "boreal". In fact, every succession starts after and intensification of the exchange of water between the bay and the open ocean. ~~We~~ Production is extremely high, and succession proceeds rapidly.

4.633 REGULARITIES IN TROPHIC AND DYNAMIC MANIFESTATIONS OF SUCCESSION

i. Concentration of inorganic nutrients.- In the course of planktonic succession, the reserve of inorganic nutrients in environment is progressively depleted, and it soon becomes suboptimal for the species that have a high intrinsec multiplication rate, adjusted to the utilization of high concentrations of nutrients. Species cap ~~able~~ (capable) of tremendous and rapid growth ~~increase in numbers~~ and of utilizing ~~taking profit fully of~~ high concentrations of nutrients are of small size and possess large ~~great relative~~ surfaces, as many minute green cells and Skeletonema.

Species able to thrive in dilute nutrient solutions, as dinoflagellates, occur ~~take advantage~~ later in succession and reduce further nutrient concentration, up to a point where replenishment or regeneration equals consumption.

Certain organisms may absorb nutrients in excess of their actual need (phosphate, for instance, in the case of Asterionella; Lund, 1950; Goldberg, Walker and Wisenand, 1951), thus depleting excessively the environment. It would seem that organisms endowed with such a power assure a longer survival for the own species and possess an ~~are at~~ advantage in succession; but it seems that part of the [illegible] nutrients leak out with the same facility as they are absorbed ~~they come in~~. Certain ~~Many~~ species, many of them of the late stages of succession, return to the environment part of the assimilated organic matter (see 3.52), but there is no clear evidence if the ~~excreted~~ matter ~~includes~~ excreted by healthy cells includes important amounts of phosphate or other essential elements. One can hypothetize that organisms belonging to later stages of succession are increasingly able to accumulate and keep biogenetic elements.

The equilibrium ~~along~~ with time between consumption and replenishment may be attained at very different levels. The very existence of an approximate steady state is particular to the mature ecosystems. ~~In the~~ Conversely a less mature stage is characterized by fluctuations in the reserve of nutrients in environment. Cushing (1959) regards the winter maximum of phosphate in temperate seas as a measure of the inefficiency of the productive cycle; a cycle, we can say, typical of an ecosystem of relatively low degree of maturity.

There are no data for generalizations about benthic communities. Communities developing on soft substrata may react cementing together loose materials (corals, encrusting algae) and reducing the surface ~~useful~~ available for adsorption

ii. Photosynthetic pigments.– There is a notable correspondence in the changes observed along the development of a confined unispecific population and along natural succession. Increase of fats and change of pigments in an ageing culture copies the changes that are observed in a natural succession and resulting here from the substitution of ~~the~~ certain species by others! By the way, this means a real superiority of the pigment extraction as a method of biological oceanography) over counting cells of different species, because changes in plant pigments cover both: 1) change in taxonomical composition of populations, and 2) change in physiological state of populations, both changes running parallel.

Quantity and activity of pigments in plankton populations.– Gillbricht (1952) gives as volumetric equivalence of 1 μg of chlorophyll, in the phytoplankton of the bay of Kiel, 0,145 mm^3 in March, 0,212 mm^3 in August, and 0,272 mm^3 in October. Data of the same author, recalculated by Banse (1956) make 1 μg chlorophyll = 0,021–0,028 mg of diatoms, or = 0,042–0,055 mg of dinoflagellates. In the Long Island Sound, Harris & Riley (1956) found a chlorophyll content of 1,07 – 1,47 % in the phytoplankton of March, with plenty of diatoms, but a mere 0,26 – 0,6 %

in May to August, in a later stage of succession, with an important participation of dinoflagellates. Riley, Stommel and Bumpus ~~[illegible]~~ (1949), for the Georges Bank, accept following equivalences for one Harvey pigment unit: in April, = 0,025 mg; in September, = 0,132 mg of organic matter in phytoplankton. ~~Our~~ Determinations in the bay of Vigo (Margalef, Durán and Saiz ~~[illegible]~~, 1955) gave, 1 Harvey pigment unit = 0,013 mg ashfree dry weight of diatoms, and = 0,039 mg ashfree dryweight of dinoflagellates of a red tide in the last stages of a succession. On the other hand ~~In disagreement with foresaid results~~, Ganapati & Rao (1958) find the ratio ~~a relatio~~n pigments: organic matter lower ~~in~~ at the t~~he moment~~ of maximum production ~~[illegible]~~, when succession begins with a diatom bloom.

Other ~~More convincing~~ evidence along similar lines of thought is brought by Yentsch & Ryther (1959a). In Vineyard Sound, ~~when state that~~ photosynthesis and chlorophyll a content are higher at the beginning of a ~~productions~~ cycle; chloroplasts occupy a proportionately larger fraction of the cell content in small diatoms, and diatoms with a wide range of cell size have roughly the same amount of chlorophyll per cell. This is a support for the often expressed opinion that nannoplankton has a productivity intrinsically higher than microplankton. In the freshwater plankton, Wright (1959) observes a reduction of the chlorophyll content per unit volume of cells, as population density increases, and also a reduction of photosynthesis per unit chlorophyll or cell volume.

The last observation points to the existence of differences not only in chlorophyll content, but also in chlorophyll activity. The existence of such differences has been confirmed by Steemann Nielsen & Hansen (1959): the rate of light-saturated photosynthesis per unit chlorophyll is higher in "sun" phytoplankton than in "shade" phytoplankton, owing probably to differences in the complement of enzymes necessary to fulfilment of photosynthesis. Future investigation may establish whether the ~~Now it remains to see, as it seems probable, if~~ late stages in succession behave ~~rather~~ as "shade" plankton.

It seems safe to assume that ~~along~~ during succession the ratio pigment weight : total weight drops steadily. The maximum relative chlorophyll content is observed in small diatoms, chlorophyceae or flagellates that ~~start~~ initiate outbursts. Changes in the chlorophyll content cannot be produced ~~only~~ solely by increased light intensity as the season advances, because, when a small bloom of diatoms is produced in summer by some local mixing, the ratio pigments : total weight increases automatically. ~~(own observations, unpublished).~~

<u>Quality of pigments in plankton populations.</u>- The change of pigment composition with ageeing of cultures has been repeatedly observed in fresh water green and blue-green algae (Halldal & French, 1958; Kingsbury, 1956; Meier, 1929; Odum & Hoskin, 1957). Old cultures, specially under deficitary nutrient conditions, store carotenes and turn yellow.

In <u>Dunaliella euchlora</u> (Ketchum, Ryther, Yentsch and Corwin 1957) the ~~quotient~~ ratio chlorophyll <u>a</u> / carotenoids is related directly to the ~~quotient~~ ratio net photosynthesis / total photosynthesis. This means that composition of pigments is related to the total capacity of production and that a higher proportion of carotenes is an index of lesser productivity. In ~~this~~ connection with this it can be ~~remembered~~ noted that Geitler (1956) considers the accumulation of carotenoids in the extremes of the cells of <u>Oscillatoria</u> as the manifestation of an internal physiological gradient, where the tips of the cells are physiologically "older" or more "mature" than the center of the cells.

~~It~~ There seems to be little doubt that the presence of pigments others than chlorophyll <u>a</u> results in a more balanced absoption spectrum and increases the efficiency of chlorophyll <u>a</u> at longer wavelenghts, ~~if~~ but not the total power output of the ~~synthetic~~ photosynthetic system.

Considerable evidence exists ~~of~~ for an increase of the complexity of the pigment system in the course of succession, with a steadily reduction of the relative quantity of chlorophyll a. Currie (1958) founds a higher proportion of chlorophyll ~~a~~ c in oceanic plankton, apparently in more mature condition. More extensive data on Mediterranean (Herrera & Margalef, 1960; Margalef, ~~&~~ Herrera and Arias, 1959) and Australian (Humphrey, 1959) phytoplankton, show clearly an increase of the relative amounts of chlorophylls b and c and of astacene, relative to chlorophyll a, as the season advances and succession proceeds ~~[illegible]~~. Yentsch (1959) finds the index chlorophyll a : plant carotenoid higher in conditions favourable to actual growth of phytoplankton, that also represent initial stages. Increase of astacene may be due, in fact, to ~~development~~ the major quantity of zooplankton, collected accidentally and extracted in the samples.

As conversion of absorption spectra to pigment concentrations should be meet with a certain caution, some would prefer to use simple empirical indices, such as the ratio of absorbancies D_{430}/D_{665} of acetonic extracts of the vegetation. The proposed index increases, in general, along succession (Margalef, ~~&~~ Herrera and Arias, 1959).

Change in the composition of photosynthetic pigments is just one aspect of chemical succession. Increase of fat content is a common character in ageing populations of algae in culture and can be described saying that accumulation of fats proceeds at a higher speed than accumulation of proteins. Yentsch & Vaccaro (1958) in cultures observe that the ~~relation~~ ratio nitrogen/chlorophyll a is related to ~~quotient~~ ratios carotenes/ chlorophyll a. Composition of pigments is related to total concentration of pigments relative to dry weight. Total concentration of pigments drops along succession, and the quantity of chlorophyll a relative to other pigments drops also. If all these relations keep a certain constancy it would be possible to introduce the notion of chemical allometry and ~~calculate~~ estimate in an approximate way, ~~[illegible]~~, the dry weight ~~is~~ as a function of certain relations observed between different pigments (Margalef, 1960b).

~~Anyway~~s Nonetheless, chemical allometry is not totally comparable to metrical allometry. Concentrations of the different substances represent actually levels of equilibrium. Pigments are continuously formed and decomposed at rates that can follow regular rhythms, f. i., daily rhythms (Yentsch and Ryther, 1957; Ryther, Yentsch, Hulb and Vaccaro, 1958). Perhaps the suggestion can be advanced that, along succession, more labile pigments with more rapid turnover become reduced in concentration relatively and to the advantage of the more stable pigments. Carotenes are, in fact, much more stable than chlorophylls, as is proved by their persistence in sinking inactive plankton and in the sediments (Yentsch and Ryther, 1959 b).

Pigments in the benthic vegetation.– So far, the pigment extraction method has been applied systematically only to the study of plankton populations, but there is no reason why it should not be useful also for the study of benthic populations. For what has been reviewed in foregoing sections, we should expect that along succession in benthic populations, total concentration of pigments drops and the composition of the pigments changes towards a reduction of the relative content of chlorophyll a.

The green algae Penicillus capitatus and Halimeda opuntia are typical of the earlier stages in the succession in the shores of Puerto Rico, and have a higher chlorophyll a content (1,8 and 1 per thousand dry weight, respectively) than Thalassia testudinum, a sea grass dominating the lasts stages (0,2 to 1,5 per thousand of chlorophyll a; Margalef & Rivero, unpublished).

The ~~quotient~~ ratio D_{430}/D_{665} amounts to 1,69 in Penicillus capitatus, 1,81 in Halimeda opuntia, 2,52 in Dictyota cervicornis and 2,11-2,42 in Thalassia testudinum. In the leaves of both, Thalassia and Posidonia, ratio chlorophyll b / chlorophyll a increases as tissues grow older, that is, toward the tips of the leaves (Margalef, 1960)

iii. Feeding relations.- Efficiency increases along succession. This is achieved through feeding specialization (stenophagy). On the way toward more mature communities , the tendency is present to substitute automatic feeding by a more effective use of information stored by the species, used to increase probability of encounters and in catching the preys. It should necessarily be so, since such information ~~is~~ can only be of use in a predictabily organized ecosystem, meaning a system that has attained a considerable degree of maturity.

Plankton.- Brachionus plicatilis feeds mostly on organisms of 3 to 6 μ, and species whose individuals measure over 10 μ are spared and unaffected by grazing (Ito, 1957). Calanus finmarchicus, on the other hand, does not ingest ~~too~~ very small cells (below 10 μ size with a slow filtration rate ~~is~~) and, moreover, can habituate itself to definite phytoplankton species. Every species has a ~~special~~ very unique feeding mechanism and the actual problems of grazing ~~assume~~ have a tremendous ~~complication.~~ complexity.

Very small cells can ~~become entrangled~~ adhere to by mucus, produced by some ~~other~~ constituents of plankton, ~~and then increase the probabilities of being grazed~~. We may speculate~~, further,~~ then on the possibility that agglutination of nannoplankton renders its utilization more effective and that agglutination is more probable when cells are not assimilating, ~~with~~ and then are lower electrical charges in the membrane (Margalef, 195~~8~~ 76). Perhaps during the night, grazing is rendered more effective through this mechanism.

Grazing exerts a selection ~~[illegible]~~ over the planktonic populations, favouring the ~~acquisition of a number of~~ species endowed with ~~either~~ adaptations (bristles, chain formation) that classically were considered as "adaptations to a floating existence" (Beklemischev, 1959; Munk & Riley, 1952). This hypothesis is substantiated by the increase of average size of cells and increased frequency of said adaptations along succession. In animals also, means of defence against predators become more and more frequent and efficient along succession.

Studies on grazing (Fleming, 1939; Cushing, 1959) show how in the first stages of succession food is wasted, being expelled after incomplete digestion. Part of this matter is regenerated and returns to the pelagic environment and part is exported to other (benthic) ecosystems.

Benthic communities.- Doty (1959) suggests that, in reefs below the level of tides, the feeding of fishes on fleshy algae may favour competition by less edible algae, such as calcareous encrusting species ~~are.~~ Such an explanation should perhaps be generalized for the common dominance of encrusting forms in final stages of many successions.

We may speculate that sea grasses, being of a terrestrial lineage, have less ~~(predators)~~ ~~enemies~~ consumers in the marine environment that algae do; in fact, marine phytophagous animals have evolved in close biochemical adjustement to the utilization of algae as food. The actual dominance of sea grasses in shore communities is to be expected, the only limiting factors being wave movement and ~~necessity of~~ light, much higher than in plants of a terrestrial origin. It is significant that most important sea-grass consumers are also of terrestrial origin (manatee, turtles).

iv. Accumulation and use of lifeless organic material.- As ecosystems mature, there is an accumulation of inactive material, with slow rate of decomposition. Dinoflagellates, at the end of planktonic successions, when they divide slowly, deposit carbohydrates as lifeless structures; thickening and complication of membrane structures is then very noticeable. the Proportion of organisms with stalks, covers, membranes, shells, increases along planktonic succession and this reduces also the probability of being eaten. A quantity of organic material is lost to the benthic ecosystem in the mineral matrix of corals and encrusting algae.

There seems to be a tendency along succession to maintain the dead matter ~~free~~ in the water at a more constant and minim~~um~~al levels.

Dissolved organic matter plays an important role in the ecosystem. Bacteri successions of species oxydizing compounds gradually ~~to ammonia~~ to nitrite, to nitrate, are examples of other possible successions, controlled by progresive alterations of certain groups of substances. Species of phytoplankton in the firsts stages of succession are, in general, "aquarium species", easier to culture in small vessels ~~and~~ with the more simple media, than species of more advanced stages, that, in in any case, did not multiply rapidly in cultures. It is becoming evident that many of these species are deficient in synthetising powers and are in need of special growth substances. (see 3.52). Interaction by ectocrine substances ~~is~~ may becom~~ing~~e increasingly important in mature stages of succession.

Many organisms excrete miscellaneous compounds detrimental to other species, that act as important agents in competition. Toxic compounds are not only inocuous, of course, to the species that produce them, but also the the species related biochemically. This helps to explain why in red water blooms, clusters of congeneric species are common (e.g., of <u>Goniaulax</u>), between which chemical competition is ineffective.

v. Mechanical transport.- In any ecosystem, individuals are more or less separated and matter should circulate between them. Diffusion and turbulence account for this in aquatic plants, less frequently the own movement of organisms. In animals, random encounters or directed exploratory movements. In any case it is possible to consider a degree of internal flow or turbulence in the transport of materials in the ecosystem; the characteristics ~~opposed~~ opposite may be termed "viscosity".

Aquatic environments can show two kinds of changes: 1) increase of turbulence and mixing of water, and 2) increase of stability with reduction of transport due to physical causes. Populations change, accordingly, adjusting themselves to prevailing conditions. But only in the second type of change, that is, under increasing stability, the organization accumulated by previous stages of the population can be rescued and new complexities historically built over it. Change of pelagic populations can be progressive or directional only if the water in which they live shows a trend toward stabilization. This is why we should speak of succession only for those changes in populations taking place when water goes from a turbul~~ence~~ent state to re of stability and not for the converse change, notwithstanding often communities seem to depend entirely upon their physical-chemical environment and to follow each other in any or (Hulbert, Ryther a Guillard, 19

Environments that afford a high degree of mobility ~~at~~ random ~~by their own,~~ cannot allow succession to proceed very far. There is a heavy drain of individuals that can be matched only by an excess of production. ~~and~~ Such a situation provides no occasion for usefulness of adaptations that have ~~related~~ to do with localization.

When succession goes ahead, random transport provided by the environment is taken over by transport provided by ~~own~~ the mobility of organisms. Movement of animals is very important in the trophic integration of an ecosystem; along succession there is a shift from great expenditure of energy in getting food to a better use of information stored by species.

In a broad manner, the trend along succession may be described as the passage from random flow to structured "viscosity".

Turbulence and plankton populations.- In the pelagic environment, strong mixing and spatial inestability are linked to the supply of nutrients from ~~a~~ ~~rowe~~ deeper levels; turbulence is essential for the unlimited maintenance of planktonic communities. It has been assumed that organisms of red water can take phosphate at one level, move phototactically to another level and excrete it here. Migration of animals can do also a certain amount of transportation upwards. But, in general, most of the movement upwards of nutrients is done by turbulent mixing , and as succession develops along decreasing turbulence, there is a net flow of biogenetic elements towards the depth.

Turbulence of water and also sinking movements of pasive organisms increase the rate of renewal of water over the cells of phytoplankters and, therefore, the rate at which nutrients are absorbed (Munk & Riley, 1952). But turbulence is a mixed blessing so far as conservation of populations concern. Turbulence reduces the adaptative value of being mobile and in so doing increases relatively the competitive chances of species devoid of ~~own~~ self-motility.

In non-mobile populations, turbulence ~~introduces a wide spectrum of movements over~~ can exert a strong influence upon the general tendency of organisms to sink. ~~By the effect of~~ through turbulence, part of the ~~cells~~ population moves ~~actually~~ upwards, and the other part sinks at a speed higher than average. If rate of increase is sufficient ~~for~~ which ~~affords~~ results in the replenishment of nutrients by the same turbulence- turbulence ~~is better~~ is better ~~for~~ for the maintenance of a population of pasive organisms, than absolute stability, where all non-motile cells can be subjected to the risk of sinking.

Turbulence accelerates the dispersal of populations to places unsuitable for life and brings phytoplankton to the ~~depht,~~ deep dark, layers of the sea. With rough weather and poorly stratified water (winter), a considerable part of the growing phytoplankton comes below the photosynthetic layers. The delay of spring bloom caused by strong mixing is well known. Not temperature, and rarely light but diffusion is the main limiting factor, and the best evidence is that where the bottom sets a limit to thickness of top mixing layer, as in bays and fjords, even with low temperature accumulation of biomass proceeds. Sverdrup (1953) developed these ideas into a working expression (see other sections of the book, 3.51, 4.61 ?), that allows ~~to~~ the calculation of a critical depth, between 1,5 to 5,5 times the compensations depth. Increase of phytoplankton can proceed only if thickness of the top mixed layer remains lower than the critical depth.

A similar way of treating the problem can be generalized by considering the losses by diffusion not only vertically, but also in an horizontal dimension, following the ideas of Kierstead and Slobodkin (1953) on the minimum size of water masses critical for the conservation of a non-vanishing population, given certain values of increase and diffusivity.

The important fact in the study of succession is that critical depth, or critical size of water mass, is a characteristic of species and of physiological status of population, since it calculations require ~~enters~~ the radiation energy at compensation depth. As the thickness of top layer of mixing becomes progressively reduced when the season advances and stability increases, new conditions of competition arouse. Briefly stated: species with a small critical depth, unable to persist at the beginning, are more and more at advantage, especially if ~~apt~~ they are capable to thrive under low nutrient concentrations.

Species of the initial stages of succession, small-celled, with a high relative pigment content, have a deeper compensations level and a high rate of potential increase. Many of them are able, as it seems, to divide also by day. But as most of the produced cells are lost to the population of the upper layers, the rate of actual population increase may be inversely related to the thickness of top mixed layer (Riley, 1942). It ~~sounds like a~~ is paradoxical that when thickness of top mixing layer decreases and the density of biomass begins to increase, the rate of cell multiplication drops.

Stability and plankton populations.– Stability is reached ~~sooner~~ earlier near the coast and in protected places and this ~~affords a~~ partially explan~~ation~~s ~~of~~ the major biomass and the more mature state of populations in such conditions. But, in other situations, especially in warm seas, vertical mixing can be stronger along the coasts than offshore and there oceanic plankton can look more mature.

~~Redue~~ Diminution of nutrients concentration and increase of stability go, in general, parallel, but not necessarily so. Increase of stability without reduction of nutrients can lead to a red water bloom. Consumption of nutrients without increase of stability can result in a practical annihilation of plankton.

Loss of turbulence means frequently the sedimentation of pasive organisms. Sinking velocities in diatoms lie, in general, between 3 and 10 meters per day. Poor nutritive conditions can accelerate sinking, since it is known that diatoms float better when assimilating actively. The problem is complex and not well studied. It seems that electrical charges of the surface of the cells in relation with the type of structural viscosity of water layers close to the membrane are important (Margalef, 1957b). ~~All makes probable~~ Such observations suggest that diatom populations sink at the end of an active periode of growth.

Active flagellates can move vertically about 2 to 10 meters in 12 hours. Movements are controlled by light; they rise by day, but can avoid too intense illumination. Even remaining at place, spinning of dinoflagellate cells can increase absorption through renewal of These organisms are dispersed and lost under conditions of intense turbulence. In ~~still~~ calm weather or under certain circulation patterns, they can congregate in superficial patches, giving the impression of ~~a~~ highest biomass. Actually, productivity is, in general, lower than in less spectacular diatom populations. Division time is usually of several days in Gymnodinium, but only of ~~2 o 1 or less days~~ 2 days or less in diatoms.

Curiously enough phytoplanktonic organisms floating in the sea through gas or oil filled vacuoles are not frequent, but ~~such~~ are common in freshwater. Certain phytoplankters remain afloat through association with mobile animals, such as <u>Chaetoceros</u> <u>dadayi</u> and <u>Ch.</u> <u>tetrastichon</u> associated to <u>Eutintinnus</u> <u>apertus</u>, and <u>Ch.</u> <u>densus</u> with <u>Vorticella</u>.

As succession proceeds, the interplay of the mobility of organisms and the stability of water result~~s~~ in an increase of spatial heterogeneity in the vertical sense~~.~~ adaptative distribution according to vertical gradients makes sense only in stabilized conditions and is ~~proper~~ characteristic of mature stages. The photosynthetic apparatus of the ecosystem becomes integrated in a more complex way, but it is soon to ~~summarize~~ determine the pattern in the distribution of pigments. It seems, notwithstanding, that the proportion of chlorophyll <u>c</u> relative to chlorophyll <u>a</u> is greater near the surface, and that the relative quantity of chlorophyll <u>b</u> (or perhaps decomposition~~s~~ products of chlorophyll <u>a</u> ?) increase toward depth.

Thermoclines and, in general, any strong gradient, act as singular boundaries in the distribution of both, sinking and actively moving plankton. The thermocline forms often the lower boundary of the distribution of dinoflagellates (Krey, 1954; Gillbricht, 1955), blue green algae in freshwater, and, rarely, diatoms. Concentrations of pasive diatoms (<u>Skeletonema</u>, <u>Coscinodiscus</u>, <u>Rhizosolenia</u>) heve been recorded in or below the thermocline (Braarud & Klem, 1931; Gillbricht, 1955; Krey, 1954). Sometimes blooms of diatoms (<u>Chaetoceros</u>)proliferate in "bubbles" of colder water protruding upwards the level of the thermocline (in Vigo; Margalef, Durán and Saiz, 1955). Summarizing, we can say that with increasing stability, the structure of planktonic ecosystems becomes more complicated.

Benthic populations.- For bottom communities, mobility of sediments has the same meaning that turbulence has for the plankton. Sand grains are shifted from time to time, exposing adhering algae (blue green algae, diatoms, Exuviaella and other dinoflagellates) to darkness, or crushing them. Algae growing in sand must have a high rate of multiplication and hence require ~~this needs~~ a considerable supply of nutrients. Mobile and phototactic organisms, such as pennate diatoms and many dinoflagellates, manage to survive in fine mud, with a lower rate of increase, just as dinoflagellates do in stabilized water.

On bigger stones, species with a lower rate of increase (encrusting algae, [illegible]) can survive and domin~~e~~ate the microscopic ones. Moreover, the development of encrusting algae and physiognomically similar organisms binds together the loose materials and reduces further the mobility of substrata, just as terrestrial vegetation fixes the mobile sands.

Animals, as ophiuroids, can move the stones laying on a muddy substratum, exposing successively different sides of them; in such conditions (Carpine, 1958) the algae (Peyssonelia) grow now here, then there, and the encrusted mass becomes globular.

Compact substrata afford better conditions than free water for an uninterrupted accretion of biomass, and a competition is possible between plankton and benthos. The densification of nutrients around the solid surfaces is an important acting factor. There are many reports of rooted vegetation in freshwater competing with plankton, and there is also experimental evidence (Margalef, 1946; Harder & Witsch, 1942) that organisms attached to the walls or lying on the bottom of reduced volumes of water displace towards them the flow of nutrients.

Water pumping by sedentary animals helps to renovate the water in contact with membranes of associated plants, increasing the rate of absorption of nutrients.

vi. Productivity, biomass and efficiency.- ~~The present section can provide a sort of summary of the meaning of succession in relation to energy flow in ecosystem~~.

Phytoplankton.- In the firsts stages of phytoplankton development, there is a higher rate of primary production and an intensive grazing, that is, a higher flow of energy per unit biomass. In the phytoplankton of the Black Sea, Morozova-Vodjanishkaja (1957) finds a relation between daily productivity and biomass of 1,7 in February, 2,2 in June and 1,2 in September. It has been discussed if the reduction in the net rate of increase of phytoplankton along succession is due more to a decrease of the multiplication rate ~~-~~ a consequence of the reduction of nutrients concentrations, or to a increase of grazing ~~-~~ a consequence of development of animals~~.~~. It may be safely concluded that both causes are at work and also that in both, rate of multiplication and rate of grazing, the trend is to reduce absolute values, minimizing the difference between them.

Benthic vegetation.- Sea grasses as Thalassia, Posidonia and Zostera have a slower turnover than algal communities preceding them in succession. The vegetation of Ulva ~~that has a pioneer character in vegetatie succession,~~ has a more rapid turnover than the later developing vegetation of Laminaria(daily productivity in relation to biomass equal to o,o4 and o,o15, respectively; Blinks, 1955. See also Odum, ~~et al.~~ Kuenzler and Blunt, 1958).

Consumers.- Flow of energy per unit biomass is related directly to the mortality rate In animals. Along succession there is a trend in the change of survival curves, towards a lengthening of the average life and drop of instantaneous mortality. The instantaneous reproductive rate (r) and mortality rate (m) define the dynamics of a population. Difference r-m is ~~null~~ zero in a steady state population,

(~~at least taken over a certain period of time~~) But similar values of the difference (r-m) can be obtained at very different levels of r and m. Of course, in a population subjected to fluctuations, the sum of the squared differences $\sum(r-m)^2$ over a certain period of time can be ~~is more or less high~~ important and implies that absolute values of r and m cannot be too low. In a population of a species closer to a steady state, with negligible fluctuations, $\sum(r-m)^2$ over the same period of time should be lower. On the other side, m is the energy flowing across the population under study and its value relative to the biomass should be made a minimum under the given conditions if success in competition and evolution is to be expected. (in the future,) ~~We could perhaps develop further~~ this point can be developed looking for ~~suggested finding certain~~ analogies in the field of thermodynamics and following Kerner's approach (1957). ~~1958) but for the moment we want to remain in a more elementary ground.~~

(2) Several exemples of successions described in the literature fit to this general pattern. Oithona and Acartia, living only a few weeks or months and whose populations have a high rate of increase and are commonly subjected to great fluctuations, are substituted in more mature stages by Calanus and by an increasing representation of long lived predatory copepods, less prone to populations explosions.

(1) Hutchinson (1957), with reference to Skellam and Brian, assumes that species with lower reproductive potential (lower absolute values of r and of m) displace the species with higher reproductive potential. The last named have always to their disposal other elements of environment, represented by "young" biotopes. Such are the called "fugitive species" (Hutchinson, 1951) or "opportunistic" species (Mac Arthur, 1960) ~~1951)~~ endowed with effective dispersal means, but inferior in competition when ~~competition~~ it is carried on in a stable and highly organized ecosystems.

<u>Efficiency</u>.- Odum and Pinkerton (1955) and Odum (1956) discussed relations between power output and efficiency in physical and biological systems, ~~finding~~ The second paper offers evidence that power output drops and efficiency increases in vegetation as light intensity drops. Probably the same happens ~~as~~ when nutrient concentrations ~~is~~ are reduced. ~~and if so, succession would be characterized by a drop of the power output and an increase of efficiency.~~ Increase of efficiency is obvious in the final stages of succession: plants with more efficient plant pigment complexes, stenophagous animals, reduction of rates of respiration and multiplication.

Grazing and preying are agents of selection that favour the survival of bigger individuals. As the trophic structure of the ecosystem is completed, new possibilities arise for a major representation of organisms of great size. Although no exact data are at hand, ~~but one develops~~ the general impression prevails that there is a ~~steady~~ continuous increase of average individual size along succession, with a drop in the relation between body surface and biomass. Relative consumption of oxygen diminishes, then, along succession. This is another aspect of the reduction of energy flow per unit biomass.

Cushing (1959) considers efficiency as the energy reaching the highest trophic level in proportion ~~of~~ to the flux passing through the sea surface. He thinks that an efficient system is characterized by a low amplitude in fluctuations along a prolonged productive cycle and a short time lag in the linkage of pulsations in different trophic levels. ~~Moreover, the members of the highest trophic level are highly dispersed in the space.~~

4.634 THE STRUCTURAL ASPECT OF SUCCESSION

i. Expression of the structure of a mixed population.- In the ~~precedent~~ preceding section (4.633) our attention was focused on the average characteristics manifested externally by the whole mixed population or by some of its structural components. The same mixed population can be considered also in terms of internal aggregation of elements or structure. The elementary unit of structure is traditionally the individual. This can present some difficulties in the case of rooted plants, of some colonial animals. Perhaps in a future approach, if structure is measured in terms of total information, it would be advisable to allow for the non uniform information content of the individuals of the different species. By the way, the information content per individual is in general higher in species proper of more mature stages of succession. Here, "information" is used in a somewhat loose sense, as something that has accumulated through successive operations of selection and that is capable of exert some influence on future events.

Structure results ~~of how~~ from the way in which, individuals fall apart in distingishable categories (species, or niches) and ~~how~~ from non-equivalent individuals distribute themselves in a certain four-dimensional pattern. For the moment, a rigorous scientific approach of the problem is lacking and only a few considerations about possible new ways can be presented. The use of individual as unit Such meaning could" not the ~~same~~ in information ~~and~~ communication theory, but ~~it is true that~~ there are considerable analogies and ideas developed in the field of information theory prove of considerable help for dealing in a descriptive and quantitative way with structural aspect of ecosystem. Perhaps it is not convenient in use a semantic areas already existing

A convenient introduction to the possible application of ~~the~~ methods of the information theory to the expression and analysis ~~of~~ of structure of populations can be gained, drawing a parallel to the problems presented by written messages. Kinds of species can be compared to number of symbols of ~~the~~ an alphabet; relative numbers of individuals in the different species can be equated to the frequencies of the different symbols.

Any given distribution of individuals into species sets up limitations to the "style" of the mixed population, whose ~~information~~ entropy content, averaged per individual, can be

$I = -\sum p_i \log p_i$

expressed as

$$I = \frac{1}{N} \log_2 \frac{N!}{N_a!\,N_b!\ldots N_i!} \qquad \text{(Brillouin)}$$

$$I = -\sum p_i \log p_i \qquad \text{(Shannon)}$$

being p_i the probability of occurrence of letter i or of species i (Shannon and Weaver 1949; Khinchin, 1957). When one state is fixed or recognized, the same ~~quantity~~ amount of information has been gained. Of course, the maximum possible information is obtained when all letters or individuals are different, a case so ~~impossible~~ improbable ~~as~~ in language as in natural populations. The minimum information is given if all individuals belong to a unique species, another improbable case only realized in artificial cultures. We will call biotic diversity the value attained by I in any given situation. This seems to ~~coincide~~ be equivalent ~~to~~ with the concept of complexity (Bray, 1958).

~~In the written language so well as in the structures of natural populations there are certain restrictions in the probabilities of neighborhood of different symbols or species, that mean a reduction of the possible information content as calculated by the previous mean. They represent a redundancy~~

This may be compared to the presence and amount of noise in a channel ~~that~~ through which there is a flow of information. In our analogy ~~such~~ the channel would be the link between successive states of a population

A very important character is given by the system of transition probabilities that link successive spatial aspects of a population. Let us consider a population of plankton in very turbulent water, where all individuals change continually and at random their positions in space. If we assume that neither births nor deaths occur, every situation contains the same information, as diversity or complexity. ~~Bray (1958) quotes the following sentence of Pringle (1951) that may be opportune: "The measure of complexity is of the statement about the system and is not the complexity of the system itself"~~.

We can compare the anterior image of turbulent plankton to a book, whose letters, without changing in nature and in their total probabilities of occurrence, would move continuously [illegible] by virtue of a sort of thermic agitation. Such a book would be, of course, impossible to read. Many communities, more like to a real book or to a machine capable of making decis~~s~~ions, have a much more stable structure, meaning that between successive aspects the probabilities of transition are much more limited. The channel has a low noise level The limitations form a set of regularities intrinsec to the population, ~~and having much to do with feedback systems~~. We would like speak of them as the order of the community (Bray, 1958).

The order, as an analogon of component of noise, entropy of change or entropy of Markov chains has to be measured with reference to time. Organization deteriorates in time. One way would be to state the relation between the number of distinguishable structures realized and the number pf distinguishable structures possible (the last is measured by the diversity or complexity) over a certain period of time. The relation approaches the unity in communities of the type of a ~~turbulent~~ plankton in turbulent water. But we can consider that the community keeps the maximum information and attains the maximum order when only one is realized of the total number of combinations that allow a given assemblage of individuals belonging to a certain number of species.

ii. Biotic diversity or complexity.-

Diversity indices.- Different indices have been suggested for the expression of biotic diversity in natural communities. Japanese workers have accepted that numbers of individuals in the different species of a natural community can be approximatively ordered in a way that approaches a geometrical ~~succession~~ progression; the ratio of the progression is an obvious diversity index. The diversity index alpha of Fisher, Corbet and Williams (1943) and the r of Preston (1948) are based on other hypothetical assumptions. ~~esis and axioms that have not been applied to the study of marine communities~~. One of the simpler diversity ind~~ex~~ices, d, is the quotient between number of species or number of species less one, and the log of the number of individuals.

vale

All the precedent diversity indices are dependent on how the empirical data fit an hypothetical distribution. An index that is free of such condition is based on information theory (Margalef, 1957a) (1958) and has the form

$$I = 1{,}443\ \underline{\ln} \frac{N!}{N_1!N_2!..N_s!}$$

where N is the total number of individuals of the sample, and N_1, N_2 ... N_s , are the numbers of individuals of species 1, 2... s. It expresses the total amount of information in bits. It is possible to calculate the information per individual, per unit volume, or the relative information to the maximum possible information content (assuming that all individuals belong to different species; or that there is the same number of species, but all equally represented). Such ~~information content is~~ a value is a measure of the information gained ~~obtained~~ when one is selected or obtained of the total number of combinations that allows the given assemblage of individuals.

Niche structure of the community.- It is customary to think of the organization of a biotic community in terms of niches.

A niche can only be defined with reference to a certain species and to a certain environment and may be represented in a multidimensional "ecological space", where dimensions represent different factors; a niche may be thought as a probability area in such a space, around a core. It can be assumed that the cores of the niche spaces for a same species in many ecosystems overlap almost completely. This is a way, perhaps too simplified, to summarize the ideas of Hutchinson (1957) and other recent wri~~t~~ters on the subject. On the other side, a dynamical approach, as emphasized by Ross (1958) is complementary. A niche is a point of transfer of energy in a community, and niches represent definite functions in the compared communities.

The relations between species occupying niches separated, partially overlapping or equal can be equated to feed-back circuits.

Between niches ~~faitly~~ separated in the "ecological space" there is a <u>negative</u>, <u>stabilizing</u> feedback that circulates information without losses, so that complexity is kept and even increased. In niches not completely overlapping, feedback (direct, or indirect through the whole ecosystem) can preserve different species by segregation and the organization of the ecosystem becomes more complex.

When the "ecological spaces" of coaching species ~~in question become closer,~~ feedback becomes null or ~~negative~~ positive. ~~and if the "ecological spaces"~~ ~~overlap completely we~~ face perfect competition and ~~a loss of~~ information or complexity is lost, ~~disappearing all species~~ but one (Gause's "law").

X (p42)

Ecosystems with partly overlapping niches have a higher number of easily interconvertible states, a higher stability in the sense of MacArthur (1955). ~~[illegible]~~ There are many alternative paths for the energy flow and the whose system can resist changes or fluctuations in the environment without collapsing, through simple active adjustement. This is common in pioneer communities. But real stability, meaning the maintenance of a ~~[illegible]~~ similar structure ~~[illegible] along~~ through time, is better achieved through segregation of niches and with energy paths without alternative possibilities and is a characteristic common in more mature ecosystems. Dunbar (1959) sees in the stable and mature tropical and subtropical ecosystems the product of a long evolution, considering that there is a steady selection at the level of the ecosystem, operating towards an increase of this sort of stability.

Changes along succession.- Changes in ~~information content~~ diversity can be ~~[illegible]~~ expected ~~[illegible]~~ in relation to development of niches. As a mixed population develops, the number of niches increases. Trophic levels are succesively added and niches gradually subdivided by segregation. Coral reefs are excellent exemples of a very mature community with an exceedingly high number of niches. This means an increase ~~of~~ in the possibilities of conveying information or keeping complexity.

~~Initial stages are impredictable; niches in pioneering communities can be considered as taken at random in ecological space, as suggested by MacArthur (1957) in a first approach to estimate the relative extension of niches (and their representation in number of individuals) in ecosystems. In mature ecosystems, extension of niches is conditioned by a complex system of feedback circuits and it is unlikely that their extension can be expressed by simple random functions.~~

× (p.41)

Gause's law seems to be generally of application to marine communities. Although Hedgpeth (1957) ~~remarks~~ points out the frequency of aggregations of closely related species in benthic communities, in one of the few exemples duely analyzed, the Conus species living in a very mature ecosystem (Kohn, 1959), a clear ecological segregation into not totally overlapping niches has been revealed. In planktonic species (Goniaulax, perhaps also in Ceratium and other genera) a strong positive generic feedback against other competitors may be at work (toxic metabolites, development of horns), and a less effective ~~positive feedback~~ competition or total absence of ~~feedback~~ competition between species of the same ~~genus and~~ niche, allows the maintenance of congeneric clusters.

The increase of the number of niches increases diversity, but this is a process that goes to a certain point and then stops. Competition eliminates all species in a niche but one, reducing diversity. The Increase of individual size along succession means a reduction of diversity or information contained in assemblages of individuals per unit biomass or per unit volume, just as a book with bigger type contain less information that ~~another~~ one with smaller ~~set~~ type. Actually there is a transfer of information along succession from the inter~~specific~~individual structures (ecosystem level) to the intraindividual level. This means that information is increasingly stored into the individuals.

Thus, from a theoretical standpoint, we have to expect the interplay of opposite trends. A trend towards increase of diversity acting at the beginning of the succession, and a trend towards decrease of diversity present all the time.

Examples ~~taken from Succession~~ relatively simple (with a small number of niches) In populations of tintinnids in the Mediterranean and of phytoplankton of the Bay of Vigo (Margalef, 1958) are consistent with ~~theoretical conclusion~~ theoretical expectations. Diversity increases at the beginning of succession, but, after "saturation" of the ecosystem, diversity drops steadily. Patten (1959) has found information (or its converse, the redundancy) to be an excellent index of the succession of phytoplankton in Raritan Bay. Total information content of a population may actually increase or not, according to ~~if~~ whether an increase in the number of individuals is stronger than the reduction of information relative per individual or relative to a maximum; but always there is a progression from low to high redundancy, meaning a reduction of the diversity. In the phytoplankton of the Sargasso Sea, summer samples, with dinoflagellates, have a higher diversity than winter and spring samples, where diatoms are dominant, and at the end of the summer period, still with dominance of dinoflagellates, there is a drop in diversity (Hulburt, Ryther and Guillard, In ~~successions~~ communities living in running waters, diversity decreases down water (Odum and Haskin, 1957); downwater communities can be considered, also by other characteristics, as more mature.

2

Diversity of a community can give valuable indications as to its place in succession. Diversity of assemblages of organisms fixed on submerged slides has been used as a criterium for pollution or fluctuations in the conditions of water. It is ~~case~~ instructive to compare diversity indices of exploited fish populations in different parts of the world. More mature ecosystems in tropical waters give higher diversity indices than fisheries ~~of~~ at higher latitudes, subjected to strong fluctuations. Pelagic fisheries have lower diversity indices than demersal fisheries. Here, diversity is chiefly related to the number of niches, ~~because we have to accept that we compare communities with a similar degree of saturation~~. In zooplankton communities, considering ~~pub~~ especially published data on copepoda, diversity is lower near the surface and close to the shore, and it seems that in the great depths diversity drops again.

iii. Order or "organization" of ecosystems.— Order is independent of diversity. A highly organized ecosystem can have actually a low diversity index. Order is related to the transition probabilities between successive stages, but ~~also~~ is reflected also in the spatial pattern. A more organized population, repeats in space small assemblages or structures, just as in a meaningful text definite groups of letters repeat themselves with higher frequencies than would be expected if independently distributed at random. Structures in a three dimensional space provide further possibilities of storing information, not given in a unidimensional sequence.

If ~~a~~ previous information has been secured, scientific prediction is more successful in a highly organized ecosystem . In these, not only the relative positions of individuals in space become more fixed or more predictable from the specific behaviour, but also their changes along time is more restricted by the existence of internal correlations, amounting to an increased efficiency of feedback circuits (reduction of time lag, etc.). Dynamics of populations (reproduction, mortality) introduce supplementary difficulties, but as irregular fluctuations are less~~er~~ in highly organized ecosystems, demographic changes are also more predictable in them.

More mature ecosystems are characterized by an increased order. As Bray (1958) writtes: " Initial stages of community development, from the time when no living organisms are present to the time when there is a fairly complete cover, show an over-all increase in order which is possible because negative change in entropy by import is greater than positive change through irreversible processes. As further development proceeds, the order of the community continues to increase, although at a progressively slower rate, until the positive change of entropy by import is equaled by the negative change through irreversible processes and a steady state is reached - a state in which entropy change is at a minimum".

Summing up, along succession, <u>diversity</u> (as an entropy) after an initial increase shows a trend to become stabilized or to decrease slightly , and entropy of change, as a measure of the contrary of <u>order</u>, decreases steadily. Along succession, the excess of production is exchanged against information, and information content of the ecosystem increases. This information is used , we may say, in building a sort of machine more able to cope with environment. At the same time, increasing amounts of information pass from structures formed by assemblages of individuals to the interior of individuals, since species ~~proper~~ characteristic of more mature ecosystems contain, on the average, more information per individual than species of ~~more initial~~ earlier conditions. The ~~cheapest~~ most efficient way to have information stored and copied is to pass it to the intraindividual level.

From a trophic-dynamic standpoint, succession goes towards the conservation of maximum biomass with minimum relative energy dissipation. From a structural standpoint, succession leads to an increase of overall information (in the sense defined in 4.634 i), stored chiefly at a level where its preservation is thermodynamically ~~cheaper.~~ more ~~efficient~~ efficient.

4.635 SPATIAL MANIFESTATION OF SUCCESSION

i. Degree and type of heterogeneity in the different stages of succession.– Plant ecologists agree that the final stage (climax) of a succession has to be understood rather as a pattern than as a~~n~~ homogenous system. Heterogeneity has a different meaning along succession: In the first~~s~~ stages, local heterogeneity originates ~~mostly~~ from random dispersal and random occupation, as is observed in fouling; this sort of heterogeneity is less organized, less ~~previsible~~ (predictable?), contains the possibility of any ~~more~~ combinations (eventually higher diversity). In later stages, heterogeneity derives from stronger segregation of niches and of precise adjustement to eventual heterogeneity in the environment. It is a more organized heterogeneity.

A pattern of heterogeneity can influence ulterior succession. Some terrestrial plants can resist~~s~~ environmental changes only if in mass, but not as disperse individuals , and it is possible that similar situations arrive in connection with coral reefs.

Greig-Smith (1957) supposes that, under similar conditions, a community showing a small scale pattern (the sort of pattern common in mature ecosystems) is more affected by environmental changes than a spatially less differentiated community. The implication ~~would be~~ is that, under a fluctuating environment, heterogeneity can~~not~~ never become so well organized.

Even the growth of a single species proceeds from a more diffuse initial condition to a sharper and characteristic pattern. The experiences of Halldal and French (1958) are very expressive in this connection. The pattern of growth of a single species of alga, cultivated in a surface, subjected to crossed gradients of temperature and light intensity, changes, acquir~~ing~~es ~~charper~~ sharper boundaries and a more characteristic aspect.

In animals, the pattern of heterogeneity changes commonly with age: Copepods are generally infradispersed, but their eggs are not (Comita and Comita, 1957). Breeding areas of sardines and other species are restricted, but grown animals can thrive in a much wider area and their mobility increases with age; if they move ~~more or less~~ at random from more populated to less populated places, a pattern of heterogeneity in the distribution of the year classes results (Margalef, 1957c). Frequently spawning occurs in less mature parts of the ecosystem, perhaps as an adjustement to a greater quantity of food and less enemies.

~~Many data on patchiness and description of distribution profiles of both, marine and freshwater, planktonic organisms have been published. Unfortunalety not enough data on benthic communities have been found available to be discussed in a comparative basis.~~

~~In open waters, more mature stages of succession~~

In the open waters, more mature stages of the succession are found in more stabilized water. Stabilization is a condition favourable to vertical heterogeneity or segregation of populations. The thermocline, as a boundary or as a place of concentration, is a supplementary source of heterogeneity. Convection cells, internal waves and other hydromechanical phenomena, occurring in stabilized situations, give origin to circulation cells, determining surface sliks and patches of free swimming organisms (Stommel, 1949; Bary, 1952). Diffusivity is lowest~~s~~ in the lasts stages of planktonic succession, so that here is a basis for the ulterior and often divergent development of every patch.

Species more mobile, bigger and less prolific, as endowed with higher diffusivity and lower rate of increase, can become more evenly distributed (Baldi, 1950). But very often their movements follow a well organized pattern (vertical migrations), so that mobility does not work against heterogeneity, but simply means the passage from random heterogeneity to organized heterogeneity. A rhythmic change in the pattern of heterogeneity is a character proper of mature ecosystems.

As a result of the interplay of several factors, heterogeneity in the distribution of almost every species results. Heterogeneities of unispecific populations combine and produce an heterogeneity pattern general for all the mixed population.

Heterogeneity is to be expected to increase towards the last stages of succession. In fact, this hypothesis has been verified in the distribution of phytoplankton in the Bay of Vigo (Margalef, 1957a, 1958). Rodhe (1959) accepts these results as generally valid for fresh water lakes also.

ii. The fine structure of heterogeneity.- The study of heterogeneity poses the problem of what has to be considered as homogeneity in mixed populations. A spectrum of heterogeneity can be constructed plotting against space (distances) the diversity -or the total information- of the community or assemblage of individuals contained in the same space. A few preliminary, partly unpublished data on phytoplankton, points that ~~in~~ normal (dare we say "homogeneous"?) ~~, or better, said,~~ populations, diversity (information (entropy) per individual) is linearly related to the logarithm of space; but further work is needed.

The same method of analysis allows the detection of changes in the pattern, ~~which will be considered as~~ indicative of true heterogeneity, ~~with~~ that can be related to the existence of some sort of boundaries. But even these boundaries, howewer sharp, did not escape to a certain degree of regularity. Around a patch of mature plankton, there is a layer with dead cells, dilution of metabolites, partial regeneration of nutrients, and the consequence would be a "skin" of plankton of less mature condition. Heterogeneity is not confusedly irregular, but organized in complex patterns, as clouds, always changing, but subjected to definite rules that are related to general dynamics of succession. Special boundaries, such as marine fronts and others, are accompanied by patterns whose degree of heterogeneity is not only dependent upon discontinuities and turbulence in the environment, but also from internal laws of development of ecosystems.

iii. Heterogeneity as a result of differential speed in succession.- For the study of the possible heterogeneous distribution of the degree of maturity in an ecosystem, we need a quantitative way of measuring it. Biotic diversity may be one. It is possible to trace maps with lines connecting the points of equal average information (entropy) content per individual, or average diversity (or complexity), the isoentropic lines, as have been called by Patten (1959).

Not always isoentropic lines give a fair idea of real maturity as assessed by the many criteria discussed in preced~~ent~~ing sections. It is possible ~~also~~ then to base such maps on compound or total indices, calculated ~~giving~~ to give to every species an index value in relation to succession or degree of maturity.

In the Bay of Vigo, a higher maturity is found in the more tranquil~~le~~ waters of protected places. In Japanese bays (Yamaz, 1955) also more dinoflagellates are recorded in the interior, likely in more stable places. It is known that diatoms are associated with turbulent eddies (Sargent und Walker, 1948) and that dinoflagellate blooms occur in patches of "old" water. In all of these instances, ~~heterogeneity~~ patchiness can be considered simply as the result of local differences in the speed of the process of succession.

A general statement about spatial dynamics of succession may be that across the surfaces connecting points of equal maturity (eventually across the isoentropic lines) there is always a countercurrent flow. Production is exchanged against organization. Less mature parts of a complex ecosystem produce in excess and give part of the production to more mature parts of the ecosystem, and at the same time become more mature. As a result, the surfaces of equal maturity move parallel to themselves in ~~the-~~ such a direction that organization is being increased in every point.

~~Capitalizing on the~~ Comparing ~~of~~ the spatial pattern in the heterogeneity of an ecosystem to the spatial organisation of an organism, we may try to compare different degrees of maturity in the communities with different degree of "maturity" in the tissues of an organism. The less organized, more primitive tissues, as the mesenchym, for instance, have a stronger turnover, can regenerate much better and ~~exchange each put against information~~ exports a surplus of materials. They are comparable to the plankton. Information is continually been stored by more inert tissues, with lower turnover and low oxygen consumption, as nervous tissue. This could be compared to benthic communities, especially to epilithic communities. Perhaps there are more basic similarities than the merely formal ones and it seems stimulating to consider the whole complex of temporal (succession) and spatial (heterogeneity) changes in ecosystems as subjected to the operation of a few principles. One of them may be: ~~the fact that~~ structures that ~~cop~~ accumulate ([illegible]) and copy information at a lesser expense have greater probabilities of survival and ~~of~~ of ~~to~~ influence the events around them.

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