A COMPARISON BETWEEN COLD-TEMPERATE AND TROPICAL INFAUNAS

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INTRODUCTION.— Quantitative surveys of the benthic infauna of shallow soft-bottoms started at the end of the last century in Denmark with the pioneer work of Petersen. His extensive studies, applying his own instruments and methods led him to the description of what he called "animal communities". These were envisioned as recurrent assemblages of animals usually characterized by few species and associated with a particular kind of sediment. The results of these studies are published in a series of papers (Petersen 1911, 1913, 1914, 1915, 1918, 1924). This completely new approach in Marine Biology gave birth to a whole series of benthic studies. Much of this initial phase of benthic research has been devoted to testing and improving the method of Petersen. The sampling instruments have been subjected to continuous modifications and today a wide array of sampling gear is in use. For the latest literature on the subject see Holme (1964), Hopkins (1964), and Longhurst (1964). The method of sampling and sample treatment are much the same as those Petersen described, although statistical evaluations have appeared to determine the effectiveness at two levels; sampling itself (distribution of samples, number of samples required per station, etc.), and sampling treatment (sieving methods, sieve mesh size and biomass determinations, etc.), see Holme (1953), Longhurst (1958a, 1958b, 1959, 1964), Ellis (1960), Ursin (1956a, 1956b, 1960), Birkett (1958), Jones (1961), Reish (1959), Lie (1965), Gallardo (1965). The end of what might be called the "classical period" in benthic research is marked by the appearance of Thorson's comprehensive account (Thorson 1957). The most recent approaches to the benthos are concerned with the study of community structure, the cycling of matter and flow of energy through the ecosystem, although in a restricted way. In community structure studies a few mathematical models have been applied. Jones (1961) was the first to use a "diversity index" to define complexity in benthic infaunas, although he mistook Margalef's index of diversity with Fisher's (Margalef 1957, Fisher **et al.** 1943). Sanders (1963) has proposed another simple model whose validity remains to be tested. The latest development in benthic ecology is the use of computers in the analysis of community structure (Parker, 1963, G. Jones in prep.) A single attempt has been made recently in U. S. A. to measure community metabolism **in situ** (Pamatmat 1965).

Surveys have been for the most part in cold-temperate areas while tropical data is exceedingly deficient and of fairly recent origin (Longhurst 1957, 1958a, 1958b, 1959; Buchanan 1958 *, Newell 1959 **, Day 1963, Gallardo in prep.). During the period from 1911 to 1957 the animal community concept passed from the status of a simple "statistical unit" to that of an "ecological unit", from being a phenomenon known only in northern waters to the concept of "parallel communities" on a world-wide basis. The latter concept as it stands today, without futher qualification, appears to be an oversimplification insofar as tropical areas are concerned. It does not describe, or account for, the contrasting features of benthic communities from cold-temperate regions and from the tropics, as will be shown later on.

The bulk of the data existing up to 1957 led to the following conclusions: 1) soft-bottom communities are essentially simple in structure, and 2) are limited in number; 3) that "the number of infauna species is roughly the same in Arctic as in temperate or tropical seas". (Thorson 1957). Day (op. cit.) has recently challenged these points, specially the last, in the light of his comparative investigations of the temperate and tropical bottoms of South Africa..

Day drew his conclusions from the following data:

	AVERAGES				
	Total nr. indiv.	Nr. Genera.	Nr. Spp.	Ratio Gen/Spp.	Ratio Ind/Spp.
West Coast (temperate) (7 samples 0.1 m²)	126	9	10	1.1	12.6
South Coast (tropical) (6 samples 0.1 m²)	42	17	20	1.1	2.1

Day saw these data as posing a problem to Thorson's conclusions, particularly the one on species diversity; and he states (p. 31) that there is a "surprising diversity of species... present in a single grab sample from the warm seas...". Day's published data does not show this very convingcingly. For one thing, the number of samples is exceedingly small. Columns 1 and 5 of Table I are important from the present author's point of view because they add support to the ideas presented below despite the reservations mentioned.

The discussion that follows deals with those features of tropical faunas that show radical differences from cold-temperate faunas as far as they are known today; in addition a tentative hypothesis is

* not fully tropical.

** not typically tropical.

presented to account for the peculiarities. This hypothesis may provide a convenient framework for the planning of future benthic studies.

It is not superfluous to add at this point that the tropical benthos, however, needs much investigation. While more than 10,000 m² have been sampled from cold-temperate regions during the last 60 years or so, little more than 100 m² have been sampled from the tropical shallow benthos.

COLD-TEMPERATE VERSUS TROPICAL BIO-INDICES.— Figures 1, 2 and 3 show the differences between cold-temperate and tropical environments using three kinds of bio-indices. The following remarks can be drawn:

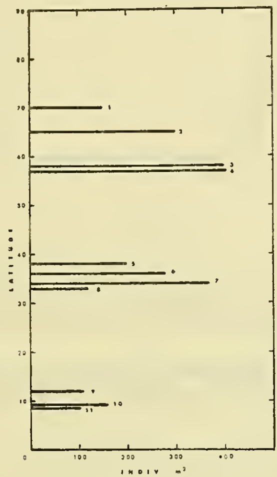

Fig. 1

a) In general, the biomass is one or two orders of magnitude larger in cold-temperate regions than in tropics;

b) the number of individuals per unit area is about one order of magnitude larger in the former than in the latter, and

c) in the case of polychaetes the mean number of specimens per species is several times smaller in tropical infaunas. This last parameter is rarely available from the literature because few workers have completed the identification of all specimens collected. The Polychaeta have proved to be one of the most important benthic groups, almost always present and generally comprising 1/2 to 2/3 of the total population; this group has therefore been used to draw Fig. 3.

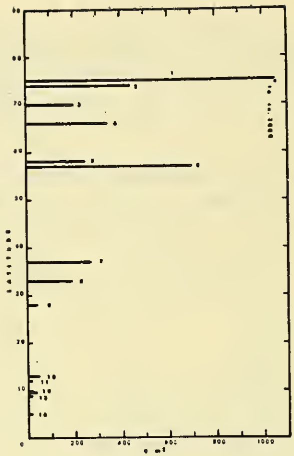

Fig. 2

After examining these data, and being cognizant of the imperfections inherent in present sampling techniques, and the errors involved when results from several authors are pooled, the questions that naturally arise are:

What is the significance of the differences in these bio-indices? What are the basic factors controlling the quantitative differences noted?

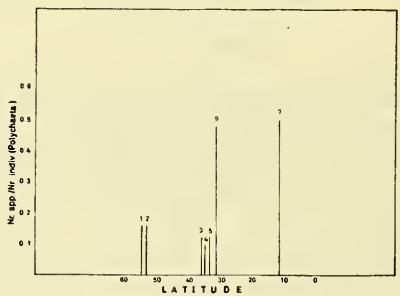

Fig. 3

TEMPERATURE AND PRIMARY PRODUCTION IN COLD-TEMPERATE AND TROPICAL MARINE COASTAL BIOTA.— Although some weight has always been placed on temperature in the sea as a zoogeographic factor, not enough emphasis has been placed on seasonal temperature ranges and their consequences, particularly in regard to the rate of turnover of matter and the flow of energy in benthic ecosystems. The present author contends that these variations have far-reaching effects in the regions under discussion. While temperatures in cold and temperate regions are either low or moderate respectively; tropical regions have high water temperatures; while the yearly range of temperature in cold-temperate aquatic environments can cary as much as 10 to 15°C *, in the tropics the seasonal range is quite small, usually about 2 to 3°C, and sometimes as low as 0.5°C in certain equatorial areas (Wyrtki 1065). Finally, while primary production may vary from practically zero in the winter months at high latitudes, to more than 1 $gC/m^2/day$ during the summer; whereas the shallow tropical waters in general have a constant organic production throughout the year (Thorson 1952, Steeman-Nielsen 1959). Steeman-Nielsen (1959: 10) further states..." It may be supposed that the high temperature of the bottom material during the whole year gives rise to a fast decomposition rate of organic material producing considerable amounts of nutrient salts". Wyrtki (1961: 48) states that... "over the shelves (of South East Asia) the cycle of nutrient replenishment is short and a high production takes place through the year in spite of only a small concentration of nutrients".

These differences are probably sufficient to account for the ecological differences of the environments being considered, and may be responsible for most of the gross quantitative variations observed.

THE PROBABLE RELATION BETWEEN THE VARYING HYDROGRAPHICAL CONDITIONS ON THE BIO-INDICES.— a) **Biomass:** Biological processes being a complex set of chemical reactions, are accordingly affected by temperature. Thus, warm shallow-water bottom animals will have a comparatively high metabolic rate. Scholander **et al.** (1953) have shown that although some arctic forms have a metabolic adaptation to cold', the oxygen consumption of tropical fishes is about four to five times higher, and of crustaceas five ot six times higher than that of the arctic forms. The rate of turnover of matter is rapid in tropical life, and animals "are also smaller and have a shorter life span" (Margalef 1963: 309; also 1955). The relation between size and metabolism has been well documented by Zeuthen (1947), and in general small animals have higher metabolic rates than bigger ones. This generality is "possibly based on the surface-volume limits to various diffusion processes" (Odum 1956). Other activities are also enhanced by higher temperatures such as predation (Thorson 1957). The constant rate of food supply from primary producers provides for matter and energy necessary and at the rate needed for all of

* High latitudes have also narrow ranges of temperature through the year (see for ex. Kondratsova 1961), but the effect of the range at such low temperatures must be considerable.

these integral functions of tropical benthic communities. Since the flow of energy and the recycling of matter is rapid, animals are selected which do not tend to accumulate the latter; therefore biomass is small. Margalef (1955) has reviewed evidence that shows that smaller individuals are selected under higher temperatures. Although data for marine benthic invertebrates is scarce, this may be another factor to consider when attempting to explain the low biomasses of tropical infaunas.

b) **Number of Individuals:** Why is the number fo individuals per unit area greater in cold-temperate regions than in tropical regions? The higher percentage of species with direct revelopment could undoubtedly account for a great part of the phenomenon if we consider the several factors that contribute to larval wastage (Thorson 1948, 1950). Another factor that will contribute to higher numbers of individuals per unit area is the longevity of most species from cold-temperate bottoms (Margalef 1955, Kuznetsov 1963), which will allow for several generations of animals to accumulate to a degree depending on the counteracting components of recruitment on the one hand, and predation and mortality on the other. In the tropics most species have pelagic development and probably reproduce throughout the year (Thorson 1952), although presumably keeping definite and particular breeding patterns (Stephenson 1934, Paul 1942, Thorson 1952).

c) **Number of individuals per species:** According to Klopfer and MacArthur (1960), the high degree of environmetal stability of tropical areas favors smaller and more restricted niches. These authors also suggest that... "with a reduction in niche size, that is, increased specialization of behavioral stereotypy, one would predict a reduction in the number of individuals per species for a given area. Where the requirements are broad rather than highly specific, that is, the niche is large rather than small, a greater density of individuals of the particular species in question should result" (Klopfer and MacArthur, op. cit. p. 294).Thienemann makes a similar statement (Thienemann 1939). These ideas are in agreement with the fact that the number of individuals per species is greater in the cold-temperate regions, and also with the smaller numbers in tropical regions.

Expressing these ideas in relation to the parameters discussed above (temperature and primary production), it is possible to suggest that where the environment is highly demanding, or unstable —cold-temperate regions— the niches will be large, requiring little relative ecological specialization, that is, high plasticity; but on the other hand also a great degree of adaptability to the environment's shifting parameters. In the tropics the adaptation requirements from the environmnt are negligible, but on the other hand this makes for high requirements of strict ecological specialization. Whether there are more niches in the latter regions (as it seems to occur in terrestrial tropical biota) than in the first is not known as far as shallow benthos goes. As we have seen above, Day, on the basis of this sampling claims that the case is for more species diversity, i. e. more niches, in the warm seas benthos. Although the writer's data from Vietnam is not yet fully worked out, they do seem to lend support to Day's views. The small number of tropical surveys and the short period that they have covered do not permit any definite conclusions at present. If we are to grant any weight to Day's conclusions, we might admit that another striking difference will be found between cold-temperate and tropical infaunas in future work, i. e. species diversity.

CONCLUSION.— It is clear from existing evidence that cold-temperate tropical infaunas differ remarkably in certain basic respects: biomass, number of individuals per unit area and ratio species/individuals per unit area. The question that naturally arises now is: What happens to the concept of "parallel animal communities" on a world-wide basis if these differences are confirmed throughout the tropical area? The concepts presented by Thorson (1957) have been confirmed in cold-temperate regions, wherever a thorough and long-term benthic study has been made. The number of comparable benthic communities described from the most varied localities in the northern hemisphere demonstrates this amply. As an outcome of this discussion it can also be seen that this concept runs into difficulties when applied to tropical areas, although data is very scanty. Will it be necessary in the future to talk of parallel cold-temperate communities on the one hand, and parallel tropical communities on the other? The fact that the bio-indices discussed differ so much demonstrates that these communities are very different ecologically, and, therefore are not strictly comparable in the framework discussed. Only by carrying out exact and standardized surveys, both in the tropics and in cold-temperate regions, can one hope to arrive at conclusions of more general validity.

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