Ecological Diagnosis of a Species and the Problem of Biological Constants[1]

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Abstract

Considers the information content of a standard systematic diagnosis of a species, and after suggesting that such a diagnosis is deficient with regard to the properties of a species as unit of ecological complexes, surveys the information required for applied science. The need for comparative ecological research is considered, especially with regard to the possibility of identifying "biological constants." The systematic and evolutionary significance of these aspects is discussed.

IN A PAPER presented to the International Colloquium on the comparative biology of marine species studied in different districts of the area of distribution (Roscoff, France June-July 1956) Kinne (1958) presented certain ideas on the ecological diagnosis of a species which seemed to us to have special relevance to the problem of general orientation of current research in marine biology. Kinne (1958) states: "We must know the *potentialities of the species as given by its specific physiological and structural constitution* freed from any inter-specific ties." This was elaborated as follows: "If we wish to advance from descriptive to causal ecology we need, in addition to a systematic diagnosis, an *ecological diagnosis of each species.* This ecological diagnosis must characterize in a few words the potentialities of a species as well as its specific demands and abilities (biological), physiological and genetical definition of a species."

These ideas had a close affinity with ideas on the same subject which the authors had been developing as part of their work and which were described by them (Kesteven, Rosa and Holt, 1958) at the same meeting. After describing briefly the objectives and methods of FAO's work with regard to living aquatic resources, they said that "The intention is . . . to accumulate information in summarized form to help make it possible to predict the distribution, abundance and other characteristics of the stocks of a given species under defined circumstances," and that "whilst fisheries biology aims to measure the values of certain gross phenotypic attributes displayed by the populations of species of economic importance, it is coming to be recognized that, for the purposes of the program for which these investigations are prosecuted, it will be necessary to consider also the mechanisms of which these phenotypic attributes are expressed and the fact that those mechanisms include genetic as well as environmental elements."[2]

Since that meeting, this work has been continued along the lines indicated and in particular drafts of "synopses" have been prepared for Rastrelliger, Hilsa, Tinca, Whales and Trichiuroidei (see Rosa, 1957, 1958) in which experimenting has been done in the reduction of published data on aquatic organisms and in the presentation of these data in summarized form. This, which has proved to be a by no means simple task, is one the authors believe is related to the important advance to be made in biology suggested by Kinne. Presented

[1]This paper was presented during the Eleventh Annual Session of the Gulf and Caribbean Fisheries Institute at Miami Beach in 1958.
[2]A small change in wording has been made in this quotation to clarify its meaning.

here is a brief account of certain of the authors' thoughts on this matter in the hope that discussion of them will bring out suggestions.

The Species Concept, and the Systematic Diagnosis

The authors do not propose to enter the lists to joust at established formulations of the species concept, but are obliged to make their own position in this matter clear since, as Kinne (1958) says in the paper referred to, "The species is not only the central point, but also the fundamental unit and measure of ecology." Basically we are with Huxley (1942) who states that "species are biological units, marked off from related units by partial or complete discontinuities" and we add to this his earlier statement (Huxley, 1940) "that they are groups which (a) have a geographical distribution-area; (b) are self-perpetuating as groups; (c) are morphologically (or in rare cases only physiologically) distinguishable from other related groups; and (d) normally do not interbreed with related groups, in most cases showing partial or total infertility on crossing with them (though neither the lack of crossing or of fertility is universal)."

In his 1942 work, Huxley quoted with approval Tate Regan's definition: "A species is a community or a number of related communities, whose distinctive morphological characters are, in the opinion of a competent systematist, sufficiently definite to entitle it, or them to a specific name."[3]

In this definition, even more than in Huxley's, the emphasis is on morphology, and rightly so for the purposes of classification. But the majority of taxonomists have held that their task was "that of detecting evolution at work" and some of them "proclaim the phylogenetic basis of natural classification" (Huxley, 1940). Other workers have held a different view and the following summing up by Huxley (1940) seems to put the issue squarely: "In the first place we may admit that taxonomic classification actually arrives at its results by evaluating resemblance and difference in the largest possible number of characters, and not by means of phylogeny, which can only be subsequently deduced, and is only measureable, if at all, in terms of the characters used in taxonomic evaluation. In the second place, however, it is certainly true that it can have what I may call a phylogenetic background, in that it can most often be interpreted phylogenetically; and, further, that such a phylogenetic interpretation may sometimes suggest an improved taxonomy. But it must, finally, also be admitted that there are certain cases where taxonomy does *not* have a phylogenetic basis."

This debate is not entered on the phylogenetic value of a natural classification. Our interest is in the discontinuities of the first part of the Huxley definition quoted above, and the dynamic characteristics of a species. However, it is suggested (and shown below) that not only is it necessary from the ecologist's point of view to add an account of the dynamic characteristics of a species to its taxonomic diagnosis, but that to do so will validly supplement the standard diagnoses in purely systematic sense, and contribute to analysis of the evolutionary processes.

It would, of course, be a foolishly extreme position to take to assert that each

[3]Despite Norman's (1948) elucidation "By the term community is meant a collection of individuals such as occurs in nature, with similar habits, which live together in a certain area and breed freely with one another" it is supposed that the term community should be replaced by a term such as population, considering the use today of the term "community" as referring to an assemblage of species.

systematic diagnosis is little more than the detailed entry on the identity card of individuals to which is applied the name lying above that diagnosis, but it is true that what is wanted is knowledge of the community function of those individuals.

In order to emphasize the point, Norman (1934) is quoted in full, a standard systematic diagnosis of a species, choosing for this purpose a species of considerable economic importance, the plaice, *Pleuronectes platessa.*

"Depth of body 1 1/2 to 2 1/4 in the length, length of head 3 to 3 7/8. Upper profile of head distinctly concave, Snout (in adults) longer than eye, diameter of which is 4 (young) to 8 length of head; lower eye a little in advance of upper; interorbital ridge low, narrow, naked or with a few embedded scales; a bony prominence in front of lower eye and often a trace of another before upper eye; a row of 4 to 7 irregular bony prominences extending from behind the eyes to commencement of lateral line, their bases sometimes connected by a low keel. Maxillary extending to below anterior part of eye, length on ocular side 4 1/4 to 4 3/4, on blind side 3 2/3 to 4 in that of head; lower jaw a little project, 2 1/2 to 2 3/4 in head. Dental formula $\dfrac{0 — 6 + 18 — 32.}{2 — 7 + 18 — 35}$ 6 to 9 gill rakers on lower part of anterior arch; lower pharyngeals broader, width 2 3/4 to 3 1/2 in length, massive, approximated for more than half their length, their inner edges angular; each with 3 rows of large, obtuse, often flat, molariform teeth, arranged close together along the inner, outer and posterior edges of the pharyngeal bone, those of the inner row being larger than the remainder; sometimes 1 to 3 small teeth in the space between the rows. Scales mostly cycloid, but often more or less spinulate in the male; occasionally a few spinulate scales present in the female; 88 to 115 scales in a longitudinal series above lateral line; 85 to 102 pores in lateral line. Dorsal 65-70; origin above or a little in front of the middle of eye; middle rays frequently with a series of embedded scales on ocular side; highest rays about 1/2 length of head. Anal 48-59. Pectoral of ocular side with 9-13 rays (3 to 9 branched), length 2 to 3 in that of head. Pelvics with 6 (occasionally 7) rays. Caudal with 19 to 21 rays (12 to 15 branched), rounded or double-truncate; caudal peduncle generally deeper than long. 2 or 3 rather short pyloric appendages and one smaller appendage farther down the intestine. Vertebrae 42 to 43 (13 + 29 — 30). Brownish or greyish, with large, rounded, red or orange (often becoming white in spirit) spots sometimes margined with brown, scattered over the body; a series of similar spots along dorsal and anal fins, and frequently 2 or 3 at base of caudal. Distribution—Coasts of northwestern Europe, from the White Sea to the Gulf of Cadiz; Iceland. Apparently entering the western Mediterranean at times. Fage (1907) records the plaice from the Balearic Islands. 'Said to attain to a length of about 3 feet.'"

Physiological and Ecological Deductions to be Made From a Systematic Diagnosis

Obviously a description such as that above bears an intense functional connotation, some aspects of which are discussed in some taxonomic papers. But the point is that the functional connotation is not normally regarded as being a significant and essential part of a systematic diagnosis. There are, however, two intellectual processes operating to withhold this information on function from the systematic diagnosis. The first is that discussed by Cain and Harrison

(1958) under the title "An Analysis of the Taxonomist's Judgment of Affinity" and by Woodger (1945) in his discussion "On Biological Transformations." "It is customary to say of two forms that they are identical as far as is known *except* in the characters, w, x, y, etc. It is then unnecessary to measure thousands of characters in which these two are indeed for the purposes of this investigation identical." (Cain and Harrison ibid.). This is indeed the customary procedure in taxonomy: one assumes that if he indicates that a particular organism is a bony fish he need not also say that it has a backbone, gills and so forth. This means that only the essential *distinguishing* features are reported, which would not be so bad if it were not that it leads to more assumptions of similarity at deep morphological level than in truth are permissible; and this process is augmented by the second, referred to by Cain and Harrison (loc. cit.) as functional and ecological correlates. It is assumed that function, as a character, is itself a correlate of the structural element by which it is subserved, an assumption which at least may omit a great deal of the story. Thus, one assumes that possession of fins signifies ability to swim, which it generally does, but other abilities also are exercised through use of fins, and Tinbergen, Baerends and others have shown much significant specificity in the use of fins as elements of particular behavior patterns (see especially Baerends and Baerends-van Roon 1950).

Perhaps at this point the authors should emphasize that they are not in any sense suggesting that the judgment of any taxonomist is being challenged on the validity of the characters chosen to establish discrimination for the purposes of classification; nor, as said earlier, do they enter the discussion of the phylogenetic interpretation to be placed on displayed differences and similarities. What is being said is that the systematic diagnosis fails to give, as it very well could, information concerning the *dynamic* characteristics of the organism. And if the taxonomist should retort, as well he might, that "it isn't meant to," we must observe, with Kinne, that another diagnosis is needed. But at the same time it is ventured that perhaps the taxonomist is missing much that is significant; and the idea is developed below that, since after all the chief characteristic of living things is that they are alive and dynamic, the elements of that dynamism, in terms of biochemistry, physiology, behavior and synecology might perhaps be real specific characters. After all, no motorist would buy a car simply on a tabulation of certain of its structural characteristics (body length and height, number and dimensions of cylinders, etc.) even if he would be prepared to assume that it would have wheels, brakes and so forth; he is in fact more interested in performance indexes, attainable speed, rate of acceleration, fuel consumption, compression ratio, road holding characteristics and so forth.

Before continuing this line of thought, however, it is desirable to consider further the information conveyed explicitly and implicitly by current systematic diagnoses. Whilst Myr (1942) has said that the number of characters considered in a diagnosis is limited only by the patience of the investigator, diagnosis of fish species generally follow a pattern, similar to that of the plaice description quoted above. They generally comprise descriptions of body form by ratios of various measurements to, generally, total length of structural features of the head with relative proportion of eye, and of features of mouth and gill apparatus, scales, fins, vertebrae, coloration. It is our view that this information could be presented, in the taxonomist's own terminology, in a way to be even more significant for the broader purposes we have in mind. Thus, in the case of body form there is an established terminology (anguilliform, depressiform, disciform, globiform, etc.) which at least more fully if not also more accurately describes the overall shape of the fish.[4] In the instance quoted above, a statement: "disciform (depth of body 1½ to 2¼ in length)" is more informative than the statement in the quotation itself. It is unnecessary here to recapitulate the results of workers such as Houssay (1912) and Breder (1926) although these would be the sources from which informative diagnoses, with regard to body shape, would be constructed. Similarly, mouth shape, dentition, fins (size, shape etc.), alimentary canal and coloration, have functional and/or ecological significance that could be succinctly indicated and which, if included, would add greatly to the information conveyed by the diagnosis.

Isolating Mechanisms and the "Ecological Potentialities of a Species"

Since most taxonomists incline to regard their classifications as signifying phylogenetic relations it would have seemed that characteristics of a species which contribute to, or influence these processes would be information proper to include in the description of the species. Since "The criterion for biospecific distinctness, for example, is whether or not two groups of individuals interbreed freely in the wild, completely irrespective of their morphological characters" (Cain and Harrison ibid.), there would be two good reasons for including in the specific description information on the mechanisms (where the two groups did not interbreed) which prevented the interbreeding: such mechanisms might themselves be of genetic origin and therefore part of the genotype, or they might be the consequence of other characters of genotypic origin; and in any case they are so close to the essence of the specific identity of the group as to be almost certainly of informational value. Mayr et al. (1953) says that the "gene pool" of which the individuals of a species are "the visible expression and temporary containers" requires "protection against outside disturbance." It is therefore relevant to submit evidence of the nature and security of that protection.

Speciation being usually discussed, in part, in terms of various isolating mechanisms classified as: geographic, ecological (ecoclimatic, ecotopic and ecobiotic), physiological and reproductive, we may consider what information regarding such systems might be included in the diagnosis of a species.

Distribution and Habitat

Most systematic papers give notes on the localities where specimens of the species have been taken but such notes characterize neither the general area in which the organism can live nor its normal habitat. Yet, its distribution is both an index of its ecological nature, *and,* in most definitions of what constitutes a species, is one of the principal indexes of its specific rank. It may not then be naive to wonder why a describer of a species is not required to specify both the general cartographic limits within which a species occurs, and its normal habitat.

For example, plaice "lives on the sandy parts of the European continental

[4]This is not to be taken to mean that the authors are advocating the elaborate verbal apparatus proposed by Gregory.

slope down to forty, or in the far north even a hundred fathoms, between the western Mediterranean and the White Sea around Iceland and the Faroes" (Wimpenny, 1953) and the "species is characteristic of sandy bottoms, where, doubtless, it can lie with the margins of the fins under the sand, or even more of the body" (Graham, 1956). Plaice is thus distinguished from the flounder which "unlike the other species of Pleuronectidae, . . . ascends rivers to considerable distances, and during an appreciable period of its life-history it exhibits a preference for brackish or even fresh water" (Jenkins, 1950), and "is found in fresh water from the ages of 1 to 4 years after which it remains in salt water" (Lübbert and Ehrenbaum, 1936). Some of the terminology is already available for this purpose (stenohaline, euryhaline, etc.) but there is need for further development; thus, there is need for a word to cover the general characteristic of salinity tolerance (or intolerance)—"halinity" presumably does not serve this purpose; again, there is need for terms to indicate whether a species spends its entire life in a single biotope (monobiotopic) or several (polybiotopic). On the other hand, although terminology exists to indicate the migrations made by polybiotopic species (see Myers), it is not used in taxonomic diagnoses.

Reproductive Habit

By this is meant the spawning place, time and behavior. Some of the differences between plaice and flounder, in these respects, are indicated by the following authorities:

Plaice: "while spawning takes place throughout its area of distribution where the water is of the right salinity the mature fish congregate in a number of spawning grounds. The diameter of the egg varies with salinity from 1.65 to 2.2 mm." (Wimpenny, 1953: Graham, 1956).

"Contrary to the Salmon, the Flounder's migration to the rivers is for the purpose of obtaining food, its seaward movement for spawning. Good catches are made in the estuaries following a frost. The fish are then heavy with spawn, which, however, is only discharged in deeper water." (Jenkins, 1950). "The Flounder's egg is one of the smallest of pelagic fish eggs (0.8 to 1.15 mm diameter; Graham 1956), the number carried by an adult female of average size is greater than in any other Pleuronectid, and probably account for the fact that in contradistinction to the other members of its family, the Flounder female is less abundant than the male." (Jenkins, 1950).

The terminology for these characteristics is available.

Population Size

Although the principal discussion of this feature is given in a later section, where its significance is treated differently, it is mentioned here because of its very great significance among the determinants of the phylogenetic processes. If it can be correct to say that there is "greater variability of common species (abundant in individuals) than of rare ones" (Huxley, 1940) and, further, that "it is important to realize that the frequency of mutant genes represents an equilibrium between mutation-frequency and selection, that variability represents a further equilibrium between recombination and selection, and that the size and structure of the population will have effects on both these equilibria," (Huxley, 1942), it must be valid also to wish to have some indication of population size in the diagnosis of the species.

Life Span

This is in the main complementary to the preceding characteristics, being an important element of vital statistics, and significant in the phylogenetic process. However, it has physiological implications and may also have relations with reproductive habit. When determined it is recorded of course very simply.

Autecological Aspects: The Species as Organism of Stabilized Biapocrisis

Although Huntsman's term biapocrisis has not gained general acceptance in ecological literature, we are inclined to the view that the *whole* for which he coined the term, ("the response of the organism as a whole to what it faces where it lives," Huntsman 1948), does require a special term. Moreover, the definition just quoted is preceded in his paper by the statement that the term was coined "in order to specify clearly what knowledge is required to predict the distribution and abundance of organisms," and since what the authors have in mind is the assembly of this required knowledge in systematic form, it is believed that a term which helps in the process of systematisation is of value, even if the biapocritic data are considered only part of the array of knowledge required for the purpose stated.

"The responses which are of primary concern are by reproducing or not reproducing, by growing or not growing, by moving or not moving, and by surviving or not surviving," (Huntsman l.c.) and, in effect, Huntsman's exposition of his biapocritic method shows it to consist of a logical and systematic analysis, employing field observations and data from specially designed experiments, of the factors determining reproduction, growth, movement and survival.

It is obvious that the assembly of these biapocritic data is of first importance for the purposes the authors have in mind, namely the prediction of distribution and abundance which, as the above quotation shows, were those of Huntsman before us. For this reason a large part of the diagnostic schedule (see Rosa (1957) Appendix 2, and Kesteven, Rosa and Holt (1958) Annex) being used in the authors' work is devoted to the bionomic and biapocritic features. It is here, perhaps more than elsewhere in this schedule, that the difficulties of reduction of data and the need to find biological constants must be resolved. But here also the authors become involved in two problems of interest to the taxonomist: physiological raciation (or even speciation) and phenotypic plasticity.

Dealing first with the matter of biological constants: In the literature are found accounts of experiments and of analysis of sets of field data from which equations are prepared expressing mathematically the relation between values of some characteristics of species under investigation and of some factors of the environment which appear to exert a significant influence on the characters of the species; these equations contain constants which characterize and give a measure of the response of individuals of the species to the selected factors at various levels of intensity of influence. Clearly the more of such constants that could be available, and the greater their reliability, the more accurate and reliable would be the description of a species. However, there is a paucity of such constants and the work on them is still uncertain because of the difficulty of disentangling the range of response of individuals of, say, a single generation in one locality, from the genotypic plasticity of the species. That differences other than morphological may establish specific status is certain, even if, for the most part, the morphological features by which the distinguishing functions are subserved should have attracted prior attention and be easier of demonstration. It is not a question of which came first (presumably in general they go together), but that for the purposes required here the non-morphological are too important to leave unreported. As example of what is meant the conclusion of a paper by McCauley (1958) is quoted: "Hart (11) concluded, in his study of geographic variations of fresh-water fish, that there was no strong evidence in his material of the existence of physiological races within species. Any physiological differences he uncovered were accompanied by morphological differences that gave each group the rank of subspecies. The findings of the present investigation are similar to Hart's observations. The two geographic groups of *Salvelinus fontinalis* which are considered to be morphologically similar did not display any difference in their lethal temperatures or in the relation of cruising speed to water temperature. The geographic groups of *S. alpinus,* on the other hand, are considered to be distinct subspecies and this classification is confirmed by the significant difference in their lethal temperature relations."

The taxonomists are likely to be a little reluctant to enter this field. "Are the 'physiological races' of insects, etc., to be given specific rank when they are partially or wholly intersterile but yet show very little morphological distinction? The museum systematist naturally shrinks from this course, as it puts the main onus of assigning specimens to their correct category, on ecological or experimental methods for which there is neither space nor time in the routine work of a museum." (Huxley 1940).

But since fishery biologists are so actively engaged in study of such matters a rich flow of relevant data is being produced each year and it might be well to give early thought to its systematic assimilation into the taxonomic apparatus.

Species as Population

In the (Kesteven et al. 1958) paper referred to at the beginning of this contribution, reference was made to the general significance of population size and, in the face of some scepticism, the authors have ventured to speculate about the possibility of each species having an intrinsic size potential. The genetic significance of population structure and size is of course unquestionable, as indicated by the earlier quotation from Huxley and by the work of Fisher, Sewell Wright and many others, but that is the other side of the coin. What we have in mind is that the sum of the biapocritic characteristics of the individuals of a species population result, among other things, in a population whose size is a constant times the value of certain features of the environment, just as is the physiological response of an individual; and the constant would be regarded as being a genotypically determined characteristic of the species (or the result of a set of such characters). Grounds for this idea are partly argument by analogy (with some reference to ideas on the super-organism), and partly evidence from comparison of differently located populations of a single species, and from comparisons of populations of closely related species in practically the same location. The argument by analogy refers to the determinants of typical size of individuals of a species. Although there is generally considerable variation between individuals of a species, within a single population, the pattern of growth, including its rate, the shape of the curve of growth against time, and the upper limit of size, lies within certain limits which are fixed less by environmental factors than by the structural and functional characteristics of the body of the individual, and the relations between them. Haldane's speculation about the breast bone of an angel, and speculative explanations for the extinction of certain giant reptiles, indicate the limits imposed upon a species once its *bauplan* becomes determined. It seems to us that similar limits are imposed on the population of a species (using this analogously with "body of an individual") once its structural and functional characteristics become determined within the context of the environment in which it lives. Of course the restrictive relations between the elements of a population are much less intense than are those of the body of an individual and relatively the variations in magnitude of a population are far greater.

Every fishery worker must have been impressed by the differences in sizes of populations of different species, even closely related, within a particular locality; many may have reached the conclusion that such differences cannot be explained by single characteristics such as fecundity or position on the food chain. Similarly each worker must have been impressed by the persistence, through areas of different size, of a ranking (in a kind of numerical hierarchy) of various species or groups. For example, most clupeoids form large populations and hold a dominant position in whatever habitat they are found.

Table 1 will serve to illustrate something of what we have in mind. This table has been developed from one published in Graham (1956) to the columns of which some figures have been added whilst adding two columns relating to catch. The data of the first catch column and the other added figures have been taken from the official publications as indicated in the footnotes; those of the second catch column have been arrived at by simple calculation from the first column and using rough average weights of the fish in this catch. These catch data are assumed, with appropriate reservations, to constitute some index of the relative sizes of the populations of the different species listed in the table; and it is clear that there is little relation between these catch figures, and hence on our assumption, between population size, and fecundity or species average size. Thus, ling has the greatest relative fecundity among the gadids, although its population is the smallest but one. Cod, of which the population is greatest, has fecundity approximately the same as that of saithe and haddock whose populations are only one tenth the size of that of cod. Nor does position on the food chain provide an explanation, as is clear from comparison of the sardine with the gadids.

Population size is usually discussed in terms of fluctuations about an unspecified absolute magnitude, and in such discussions it is assumed that certain environmental factors, density-dependent or density independent or both, relax and contract the limitations they impose on each population and cause declines or permit expansions: it is of little value to say that this means that if these restrictive factors were removed from bearing on a population it would continue to increase without limit. Such speculation can be thrust aside because these populations exist within strict limits imposed by biotic and abiotic factors and because the effect of these limits is not the result only of the intrinsic character of these factors, but also of properties of the species. The factors of the environment of a particular species that permit the play of its potentialities, and place restrictions on them, exercise their influence on the population through and by

TABLE 1

COMPARATIVE TABLE OF FECUNDITIES AND CATCHES

Taxonomic Groups	Catches Weight[4] (in '000 k)	Catches Numbers (in '000)	Fecundity[1] Range	Individual[1] Weights (g)	Individual[1] Lengths (cm)	Fecundity per 10 g fish
Gadidae —						
Ling	44,515	5,560	12-28 million	8-24 k	45-61	12,000
Cod	2,690,342	672,000	1.8-9 million	4 k[2]	60-70[2]	4,500
Saithe	257,586	64,300	2-8 million	4 k[2]	55-70[2]	5,000
Haddock	331,738	94,700	12,000-3 million	80-6,900 k	22-85	4,500
Tusk	23,444	—	0.75-2.25 million	—	—	—
Bothidae —						
Turbot	7,134	1,110	8.1 million	6,4 k	—	12,700
Pleuronectidae —						
Flounder	11,245	21,000	0.56-1.6 million	348-723	27-38	22,000
Plaice	98,743	76,000	16,000-346,000	125-2,580	23-61	1,500
Clupeidae —						
Sardine	224,902	6,420,000	15,000-55,000	17-53	13-19	10,000
Herring	2,812,665	22,300,000	12,000-33,000	103-150	21-29	2,200
Ammodytidae —						
Sand-eel	112,000[3]	8,000,000	13,350-36,300	8-20	14-18	18,000

[1]Graham (1956)
[2]Ann. Biol. Copenhague, (1956), 13, 1958.
[3]Seventh Meeting Permanent Commission, International Fisheries Convention (1946) (mimeo.), 1958.
[4]Bull. Statist. Pêch. Marit. Copenha., (1956), 41, 1958.

virtue of the characteristics of the species itself. Heat is of itself not intrinsically lethal, its levels are favorable or unfavorable for each species because of the characteristics of the tissues, cells and proteins of the species. This is true of all factors that influence the functioning of a species, and it would seem that among a group of biocoenotically similar species, that one whose population is greatest is the one whose characteristics constitute a mosaic making greatest use of each of the factor-ranges offered by the environment.

Consider the matter from another viewpoint. It is known from research work among birds that there are lower levels of population density below which maintenance of the population is impossible; below these levels certain ethological and physiological conditions are not met. This situation then (apart from the circumstances that depressed the population below the critical level) is chiefly a result of the intrinsic characteristics of the population. At the other extreme it is known from work, chiefly on insects but also on populations of small animals of other phyla, that populations within restricted environments establish equilibria whose levels are determined by certain limiting factors so that, no matter how liberal may be the supply of certain materials, or how favorable certain factors might be held by the experimentalist, the population fluctuates about a level determined by the limiting component or factor. The timing of the supervention of limiting factors for any population, or the rate at which the limiting values are approached in the course of the change from one level to another, is determined in some cases by external factors and in others by factors within the population itself. The latter group of factors is not adequately represented by situations of "arithmetic" character such as metabolite accumulation in closed or partially closed systems of simple populations; a better example is that of the inhibition of the growth of slowly growing members of a population by substances released by the larger, more rapidly growing members of the population, demonstrated by Rose (1959) in the case of tadpoles and fish the essence of which is that the arithmetic increase itself generates changes in other components whose influence increases geometrically. Again we arrive at the concept of the fitness of the species to its environment with respect not only to the structure and functions of its individuals, but also to its population magnitude; and, we must assume, to the structure and dynamics of the population.

Furthermore, recollecting the laboratory experiments with populations of small animals, and referring to earlier remarks about the impossibility of postulating completely relaxed environmental factors, we may assert that no natural biotope is limitless.

Apart from the general biological implications of Kinne's suggestion and of the development of that idea here, two immediate applications for this concept are seen. Firstly, if the population characteristics of a species can be considered in this way then there is available a method of systematic approach to description and appraisal of living aquatic resources and effective extension of the established techniques of cataloguing species. Secondly, and similarly, this concept has important relevance to proposals for transplantation of species: such operations need not be intelligent guesses but informed prognoses.

LIST OF REFERENCES

Baerends, G. P. and J. M. Baerends-Van Roon
1950. An introduction to the study of the ethology of cichlid fishes. Behaviour, Suppl. *1:* 1-243.

BREDER, C. M.
1926. The locomotion of fishes. Zoologica (New York), *4* (5): 159-297.

CAIN, A. J. AND G. A. HARRISON
1958. An analysis of the taxonomist's judgment of affinity. Proc. Zool. Soc., Lond., *131:* 85-98.

GRAHAM, M.
1956. [Ed.], Sea Fisheries: their investigation in the United Kingdom. E. Arnold (Publishers) Ltd., London, 487 pp.

HOUSSAY, F.
1912. Forme puissance et stabilité des poissons. Coll. Morphologie dynamique, Paris, *4:* 1-372.

HUNTSMAN, A. G.
1948. Methods in ecology—Biapocrisis. Ecology, *29* (1): 30-42.

HUXLEY, J.
1940. [Ed.], The new systematics. Oxford Univ. Press, 583 pp.

HUXLEY, J.
1942. Evolution: the modern synthesis. Allen and Unwin Ltd., London, 645 pp.
1958. International Council for the Exploration of the Sea, Bull. Statist. Pêch. Marit. Copenhagen, (1956), *41.*
1958. Ann. Biol. Copenhague, (1956), *13.*

JENKINS, J. TRAVIS
1950. The fishes of the British Isles both fresh water and salt. F. Warne and Co. Ltd., London and New York, 408 pp.

KESTEVEN, G. L., H. ROSA, JR. AND S. J. HOLT
1958. A note on abundance and distribution of marine organisms of economic importance. Inter. Un. Biol. Sci., Ser. B, (24): 287-297.

KINNE, O.
1958. A programmatic study of comparative biology of marine and brackish water animals. Inter. Un. Biol. Sci., Ser. B, (24): 87-92.

LÜBBERT, H. AND E. EHRENBAUM
1936. Handbuch der Seefischerei Nordeuropas. II. Naturgeschichte und wirtschaftliche Bedeutung der Seefische Nordeuropas. E. Schweizerbart'sche Verlagsbuchhandlung (Erwin Nägele) G.m.b.H., Stuttgart. 337 pp.

MAYR, E.
1942. Systematics and the origin of species. Columbia University Press.

MAYR, E., E. G. LINSLEY AND R. L. USINGER
1953. Methods and principles of systematic zoology. McGraw-Hill, New York, 328 pp.

MCCAULEY, R. W.
1958. Thermal relations of geographic races of *Salvelinus.* Canad. J. Res. (Zool.), *36:* 655-662

NORMAN, J. R.
1934. A systematic monograph of the flatfishes (Heterosomata). I. Psettodidae, Bothidae, Pleuronectidae. Brit. Mus. (N.H.), London, 459 pp.
1948. A history of fishes. A. A. Wyn, Inc., New York, 436 pp.

PERMANENT COMMISSION, INTERNATIONAL FISHERIES CONVENTION 1946
1958. Seventh Meeting, (mimeo.).

ROSA, H., JR.
1957. Synopsis of data on the species of the genus *Rastrelliger* (Jordan and Starks, 1908). IPFC Meet. Sub-Comm. on Rastrelliger, Malaya, September 1956, (mimeo.).

1957. Synopsis of data on hilsa *Hilsa ilisha* (Hamilton-Buchanan) 1822. IPFC 7th Session, Bandung, Indonesia, May 13-27, 1957, (mimeo.).
1957. Synopsis of data on whales. (mimeo.).
1957. A synopsis of biological data on the species of *Trichiuroidei.* (mimeo.).
1957. The survey of living aquatic resources. Proc. Gulf Caribb. Fish. Inst., Florida, 9th Ann. Session, Bahamas, Nov. 1956. pp. 153-170.
1958. A synopsis of biological data on tench *Tinca tinca* (Linnaeus, 1758). (mimeo.).

ROSE, S. MERYL
1959. Failure of survival of slowly growing members of a population. Science, *129* (3355): 1026.

SCHUSTER, W. H.
1958. Synopsis of biological data on milkfish *Chanos chanos* (Forskal, 1775). IPFC 8th Session, Colombo, Ceylon, Dec. 6-22, 1958, (mimeo.).

WIMPENNY, R. S.
1953. The plaice. E. Arnold and Co., London, 145 pp.

WOODGER, J. H.
1945. On biological transformations. In: *Growth and form. Essays presented to D'Arcy Thompson* ed. W. E. Le Gros Clark and P. B. Medawar. Oxford: Clarendon Press.