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On Bird Species Diversity

Author(s): Robert H. MacArthur and John W. MacArthur

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regeneration, and at the end of the experiment had undergone no noticeable increase in length. Variable results were obtained with those treated with a concentration of 0.05 N; in 2 salamanders regeneration occurred whereas in one it was completely inhibited. Thus, the latter concentration is too weak to produce consistent results and therefore not well suited for use in field studies.

Although beryllium has been known to cause edema and even death (Thornton *op. cit.*), the single death resulting from unknown causes in the present study is not believed to be attributable to the beryllium treatment as the animal was subjected to a concentration of only 0.05 N (the lowest one used). Animals treated with higher concentrations did not show any ill effects. However, in field studies it would be advisable to use the lowest concentration effectively preventing regeneration (in this species,

0.1 N), thereby minimizing possible undesirable effects caused by high concentrations.

A suggested procedure for field work is to carry a block of wood with holes bored in it to accommodate a vial of beryllium nitrate and several vials of water for rinsing off excess chemical after treatment. The block provides a firm support and prevents spillage caused by movements of the salamanders' feet. Treatment is also facilitated if the vials have sufficiently small mouths that undue movement of a salamander's foot is prevented while it is immersed in the solution.

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ON BIRD SPECIES DIVERSITY

ROBERT H. MACARTHUR AND JOHN W. MACARTHUR

Department of Zoology, University of Pennsylvania and Marlboro College, Marlboro, Vermont

It is common experience that more species of birds breed in a mixed wood than in a field of comparable size. It is also well known that tropical forests seem to support more species than their temperate counterparts. These facts are often explained in terms of the number of "niches" or "ways of life" which the habitat provides. In this paper, a somewhat more precise analysis is attempted.

The actual number of species is better replaced by a number called the "bird species diversity," calculated as follows: Let p_i be the proportion of all of the bird individuals which belong to the i th species. Then the bird species diversity, is $-\sum_i p_i \log_e p_i$. This is a

formula used by communication engineers to calculate the information generated, *e.g.*, by a typist who uses the different keys with frequencies p_i . Thus, for instance, a one species community always has zero diversity; 2 species, one with 99 individuals and one with 1 individual, will have diversity of $-.99 \log_e .99 - .01 \log_e .01 = .046 + .010 = .056$ (close to zero), while 2 species each with 50 individuals will have diversity of $.347 + .347 = .694$. This illustrates why diversity is a better measure than actual number of species, for the community with 99 of one and 1 of the other seems closer to the community with one species. Margalef (1957) has frequently used a similar measure in his plankton studies. In terms of this, the question becomes: "What is it about the environment which controls the bird species diversity?"

One more refinement of the general problem is necessary. For, even if all the bird species were equally abundant, a bird census of a small area (say an acre) would have only a few of the species. Since an acre supports 3 or 4 pairs of birds, not more than 3 or 4 species could be expected to have nests in the given acre. And if the area is so homogeneous that adjacent 1 acre (say) territories are occupied by the same 3 or 4 species, then the whole area cannot have more than 3 or 4 species. This is contradicted by the abundant evidence that stands of vegetation with the degree of homogeneity resulting from a uniform history of cutting

and other interference have very many (up to 106 at least in Mexico—Davis (1955)) species of breeding birds. Therefore, of course, the territories of most species are scattered rather sparsely over the area and the territories of very few species form a mosaic. It must be concluded that either the species are scattered randomly over the habitat, or else, more plausibly, that birds use some fairly subtle differences in local habitat as criteria for habitat selection. Returning to the bird species diversity, it clearly can increase as the area increases. Since there is no adequate theory of "species-area" or "diversity-area" curves, all censuses must cover approximately the same area so that variations in the bird species diversity reflect differences in habitat composition rather than variations in size of census area. Although many of the censuses reported here were taken over larger areas, the breeding bird populations of a randomly chosen 5 acres of each will be compared.

The procedure of the research described here was to census a wide variety of habitats, differing in (1) plant species composition, (2) foliage height profiles, and (3) latitude, and to determine how much each of these factors influenced the bird diversity.

MEASUREMENTS

Plant species composition was measured by an index of plant species diversity computed with the formula used for bird species diversity. p_i now refers to the total area of the leaves of the i th plant species, expressed as a proportion of the total leaf area of all of the species on the census plot. It would be a formidable job to measure areas of individual leaves, but fortunately a much easier and more accurate method bypasses this: Imagine all the leaves lying on the ground as in the autumn. If there are, on the average 4 layers of leaves on the ground, then there are 4 acres of leaf per acre of this habitat, and if we were to push a sticky needle through the fallen leaves at random points, then an average of 4 leaves would adhere to it. And the areas of the leaves are automatically taken into consideration so that if $\frac{1}{4}$ of the leaves picked up were of some large leafed species, it would indicate precisely the

same total leaf area of that species as of a small leafed species whose leaves were picked up with the same frequency. Rather than wait for the leaves to fall, it is easier to erect a stiff wire and count the leaves it touches (since leaves on trees do not lie horizontally, some error is introduced in this way, but it gives a convenient approximation). For the canopy, rather than using a wire, a sighting was made vertically through a 10 foot aluminum pipe of 1¼ inch diameter and the number of leaves which a wire would intersect was estimated.

For coniferous trees, and sometimes for deciduous, it seems preferable to use fraction X of sky not obscured by foliage and estimate the number n of leaves which a wire would intersect by the formula $e^{-n} = X$ which is the first term of the Poisson distribution.

Thus, if 90% of the sky is obscured by foliage a fraction equal to $1/10$ is unobscured and since $e^{-2.3} = 1/10$, this is equivalent to an average of 2.3 randomly placed leaves (of any size!) above the point from which observation was made. In future measurements vertical photographs analyzed by a recording microdensitometer will be substituted for the more subjective estimates of percentage. Since leaves may not be randomly placed this is obviously only an approximation, but in practice it seems quite accurate.

From the foliage height profiles a number called the foliage height diversity was calculated using the same formula ($-\sum p_i \log_e p_i$) as before. In this case p_i is the proportion of the total foliage which lies in the i th of the chosen horizontal layers. The profiles were constructed as follows: At a sequence of heights above

the ground a white board, marked in squares, was moved horizontally away from an observer at the same height until $1/2$ of its surface was obscured by leaves from the observer's view. In forests, the board atop a high pole was erected at trial distances from the observer until an acceptable one was found. The distance D between the observer and the board was then measured and the foliage density k at that height was estimated from $e^{-kD} = 1/2$ or $k = \log_e 2/D$.

This formula too is only approximate, but seemed satisfactory. Roughly it is derived as follows. The area of leaf silhouetted against the board will be nA , say, where A is the area of the board and n is the leaf silhouette per unit of board area. The volume of space in which these leaves lie is DA , so the leaf silhouette area per unit of volume of space is

$$\frac{nA}{DA} = \frac{n}{D} = k.$$

As before, n can be estimated by the first term of a Poisson distribution so that $e^{-n} = 1/2$ or $n = \log_e 2$. The method assumes that the proportion of leaf area which is similar in all 3 layers. The size of the board is thus unimportant (since the A 's cancel out) except that a large board gives an average over more vegetation (10" × 18" was used in most of this work). In each plot, at least 16 such measurements were averaged at each of the following heights above the ground: 6", 2', 5', 10', 20', 30', 45', 60'. A profile of foliage density was drawn by eye passing through each of these calculated points. The profiles of the primarily deciduous areas censused are shown in Figure 1. (The Florida

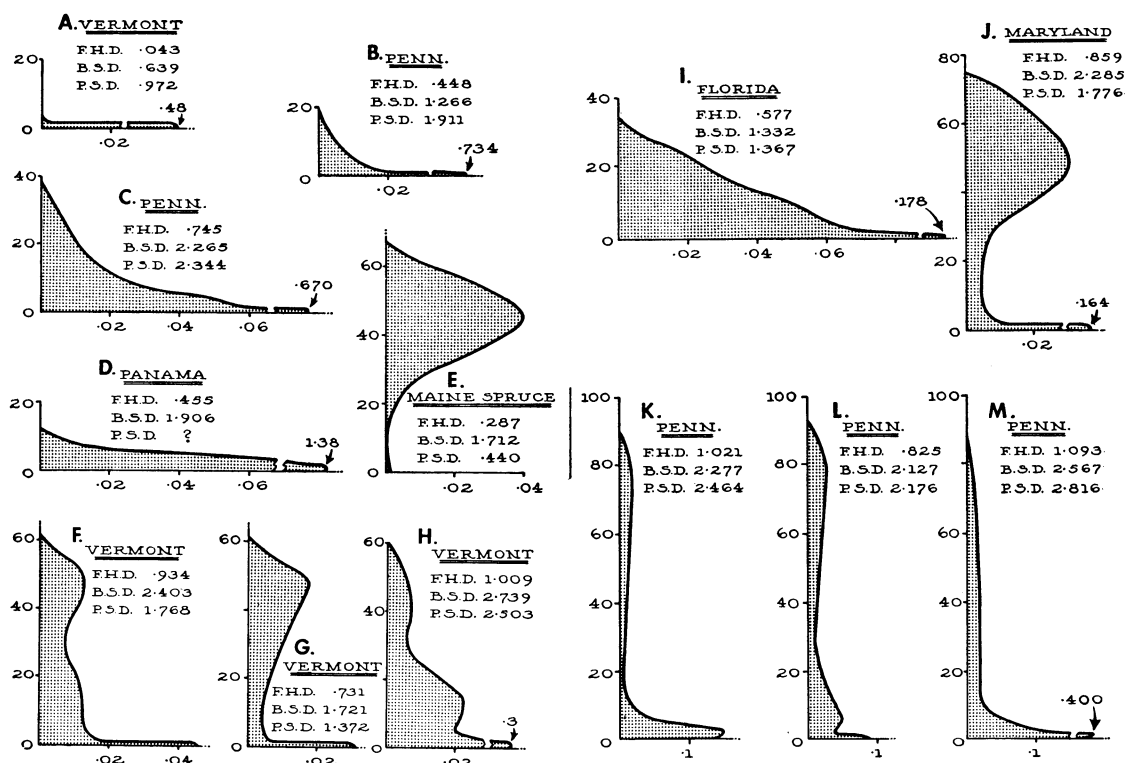


FIG. 1. The densities of foliage (measured in square feet of leaf silhouette per cubic foot of space) are plotted along the abscissae. The height in feet above the ground is the ordinate. F.H.D. is foliage height diversity, B.S.D. is bird species diversity, and P.S.D. is plant species diversity.

bird census was taken by Wolfenden *et al.* 1959, who kindly allowed measurements to be made in this area). The area of the profiles is divided into 3 horizontal layers and the proportions of the whole that each constitutes is the p_i used in the formula.

RESULTS

The actual censuses are in Table I, in which the number of territories, or fraction of territories, is entered.

The layers 0'-2', 2'-25' and over 25' are marked on the profiles in Fig. 1 and the corresponding foliage height

TABLE I. Numbers of breeding bird territories per 5 acres for the regions shown in Fig. 1

	A	B	C	E	F	G	H	I	J	K	L	M
mourning dove.....												1
yellow billed cuckoo.....									.5			
r. t. hummingbird.....					.5							.5
flicker.....			1							1		.5
red-bellied wood pecker.....						1			.5			
yellow-bellied sapsucker.....						1						
hairy woodpecker.....						1	.5					
downy woodpecker.....									1	1		
crested flycatcher.....								1	1		1	
acadian flycatcher.....									1.5			
wood pewee.....										2	2	1
olivesided flycatcher.....							1.5					
blue jay.....										1	1	.5
black-capped chickadee.....				1			.5					
tufted titmouse.....									1.5	1.5	1	1
white-breasted nuthatch.....						1					1	
brown creeper.....				1								
winter wren.....						1						
catbird.....			1							1		1
robin.....					.5		.5					
wood thrush.....										1	1.25	
olive-backed thrush.....						2						
veery thrush.....							1					
gnatcatcher.....								1				
golden-crowned kinglet.....				1					1			
white-eyed vireo.....										1		
yellow-throated vireo.....								1				
red-eyed vireo.....				1	3	1			2.5	2	4	1
black and white warbler.....							.5					
prothonotary warbler.....									2			
blue-winged warbler.....			.5									
Nashville warbler.....							1					
parula warbler.....								1				
magnolia warbler.....				.5	1.5		1.5					
black-throated blue warbler.....						1						
myrtle warbler.....				2			5					
black-throated green warbler.....				5	1							
blackburnian warbler.....				1	2	1						
bay-breasted warbler.....					3							
prairie warbler.....			2									
ovenbird.....					1.5					3	3	
Kentucky warbler.....								1		1		.5
mourning warbler.....							.75					
yellowthroat.....	1		2.5				3					2
yellow-breasted chat.....			2									
Canada warbler.....							2					
redstart.....				1	1.5			2				
grackle.....												1.5
scarlet tanager.....							.5					
summer tanager.....								2				
cardinal.....				1						1		1
indigo bunting.....					1.5							1.5
goldfinch.....	1	.5										
towhee.....		.25	1.5				1				1	1
slate-colored junco.....					.5							
field sparrow.....	2	1	3				1					
white throated sparrow.....												
song sparrow.....			.5									1

diversity and bird species diversities are shown as well as plant species diversity and latitude. These are plotted as a graph in Figure 2, showing a close fit to the line:

bird species diversity = 2.01 foliage height
diversity + .46,

calculated by least squares. Various other subdivisions of the profile into horizontal layers were tried, and the layers 0-2', 2'-25' and > 25' were chosen as those layers which made the collection of points on the graph most orderly. It is of interest that this subdivision was chosen after the Vermont censuses were taken in 1959 and that it continued to be appropriate for the censuses in 1960, elsewhere. Such subdivisions as 0-3', 3-30' and > 30' were nearly as good, but more nearly equal subdivision (e.g. 0-15', 15'-30', > 30') made a very scattered

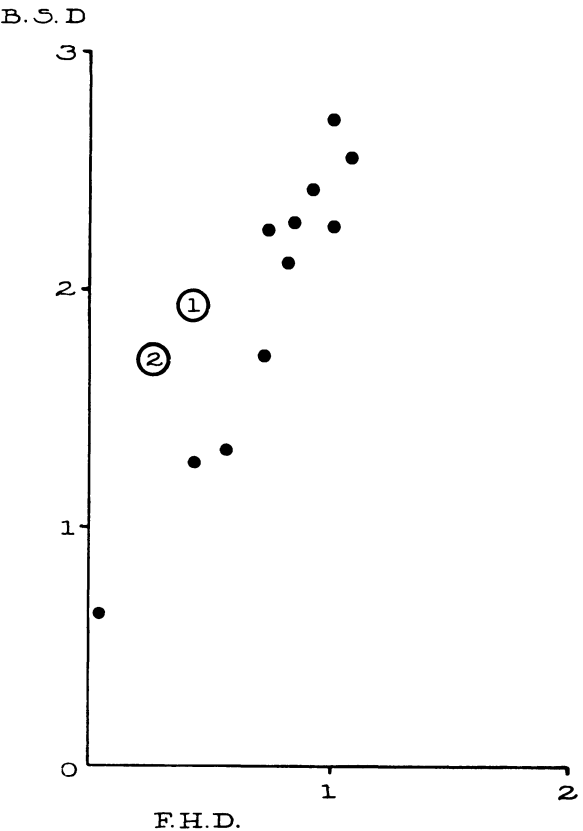


FIG. 2. Bird species diversity is plotted against the foliage height diversity of deciduous forest plots. Point 1. is census D of tropical savannah and point 2 is census E of pure spruce forest.

graph. The linearity of the cluster of points indicates that the addition of a new layer of a given amount of foliage results in the same increase in bird species diversity, (not however the same increase in number of bird species) no matter which layer (0-2', 2-25' or > 25') is added, and no matter which other layers are present to begin with. Thus, we can say that the layers 0-2', 2'-25' and > 25' are roughly equally important to the birds. (The reasons for this will be discussed later.) Looked at from this point of view, we can see the trouble with the other subdivisions. For definiteness, consider 0-15', 15'-30', > 30'. Adding a 0-15' layer to a habitat without it causes a much greater increase in bird species diversity

than the addition of the layer $>30'$. There is nothing biological about the number of layers chosen. Four or 5 layers in a roughly similar subdivision would be more cumbersome to analyse but would presumably be even more accurate. In particular, the layers $0\text{--}\frac{1}{2}'$, $\frac{1}{2}'\text{--}6'$, $6'\text{--}15'$ and $>15'$ suggested by Elton and Miller (1954) allow a rather good prediction of the bird species diversity.

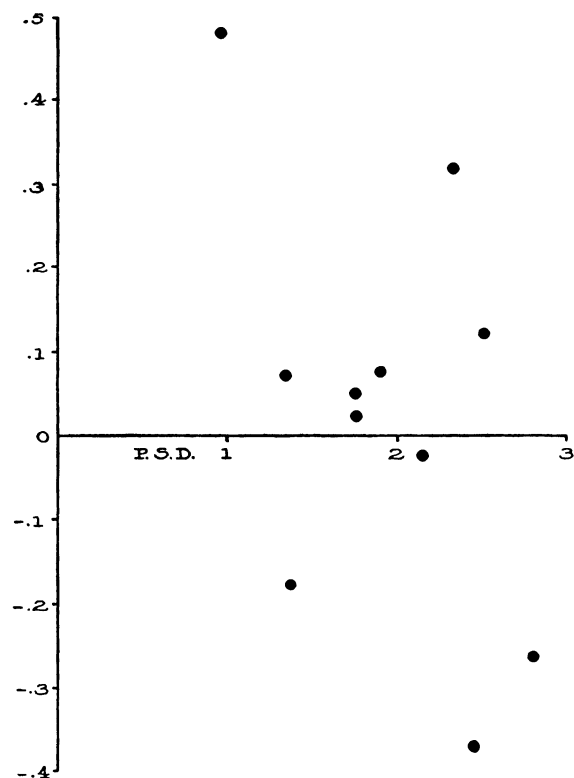


FIG. 3. The ordinate is the residual scatter, after partial regression of bird species diversity on foliage height diversity. This is plotted against plant species diversity, showing that knowledge of plant species diversity does not provide additional knowledge of bird species diversity. The least squares equation was $B.S.D. = 2.546 F.H.D. - .152 P.S.D. - .250$, and the residual scatter was computed from the formula $B.S.D. - 2.546 F.H.D. - .048$.

The next question is: How much of the remaining scatter, *i.e.* how much of the variability in bird species diversity not accounted for by the variation in foliage height diversity, can be accounted for in variations of plant species diversity and latitude? Remarkably enough, the answer is "None." This is seen most easily by glancing at Figure 3 which shows that the residual scatter after partial regression is more or less independent of plant species diversity. Thus, although plant species diversity alone is a good predictor of bird species diversity it is because plant species diversity is high when foliage height diversity is high, and, when this is taken account of, plant species diversity can contribute nothing further. In other words, habitats of the same profile have the same bird species diversity whether composed of few or many plant species. As a striking example of this, the almost pure stand of white spruce

on Mount Desert Island in Maine which the authors studied earlier (MacArthur 1957) had as great a bird species diversity as the forests of very mixed composition in Pennsylvania and Maryland.

The lack of effect of latitude is puzzling but is only tentative since a rather poor sample of latitudes have been examined. Furthermore, a brief trip to Panama yielded a tentative bird species diversity in a savannah area of 1.906 and foliage height diversity of .455 (see Fig. 2). Thus, the tropical bird species diversity is much greater than the temperate one for habitats of comparable profile. The excess of tropical savannah over temperate fields is about equal to the excess of the bird species diversity in the tropical forest over temperate forests. These facts will be discussed further in a separate paper.

DISCUSSION

These results are rather statistical in nature. What is their meaning in terms of individual birds or species? The simplest explanation which seems to account for the observations, describes the "shape" of a bird's niche. Let us return to the picture of many territories distributed over an area and consider the following evolutionary argument. A large number of species can be accommodated in an environment in a variety of ways of which there are 2 extremes. Each species may have different habitat preference and feed throughout this habitat on all kinds of food, or, all species may share the entire habitat, each species feeding on a different variety of food or in a different situation within the habitat. The first extreme violates what might be called the "jack of all trades—master of none" principle that natural selection favors the increased efficiency resulting from a certain amount of specialization. In the other extreme, specialization has proceeded so far that time and energy are wasted in travelling between spots for which the specializations are adapted. It is hard to say just where the balance of these opposing requirements would be reached, but it is clear that greater specialization resulting in increased efficiency would always be favored as long as no time or energy are wasted. And no time or energy will be wasted if niches are "convex" in the sense that between any 2 fairly distant feeding places there will be a fairly natural route also consisting of feeding places. A specialization to a single tree species in a mixed forest would clearly violate this since, in passing from one suitable tree to another, the bird would go through many unsuitable ones. Thus, natural selection would tend to eliminate a situation in which bird species diversity depended upon tree species diversity, unless, as in some fruit eating species, a very remarkable improvement in efficiency is achieved along with the restriction in feeding position. Thus, one principal result of these censuses can be predicted on assuming that niches are convex.

Next, we may ask "why are the layers $0\text{--}2'$, $2\text{--}25'$, $>25'$ equally important? Is it because birds respond to different heights, or is it because they respond to different configurations of vegetation in different layers?" In the latter case, herbs, bushes and trees presumably correspond to the layers $0\text{--}2'$, $2\text{--}25'$ and $>25'$ respectively, although small trees count as bushes etc. There is good evidence for this latter explanation. For, although deciduous forests vary principally with height above the ground and hence have a bird diversity predictable from the height profile, conifers (especially spruce) have a marked "inside" and "outside" for which

species are specialized (MacArthur 1957). Hence bird species diversity would be high in a mature spruce forest even if few layers were present. This is precisely what happens in the Maine white spruce wood mentioned earlier, with bird species diversity of 1.712 and foliage height diversity of .287 which is seriously off the graph of deciduous forests (Fig. 1).

A different way of looking at the data gives additional insight. Watt (1947) has pointed out that plants are distributed in patches. Hutchinson and MacArthur (1959) attempted to explain the sizes of coexisting organisms in terms of an environment composed of a mosaic of kinds of patches. Different combinations of patches formed the habitats selected by different species. The present research can be easily interpreted in terms of this picture of the environment. In fact, our results suggest that the patches forming the birds' environmental mosaic are sections of canopy C (over 25'), patches of bushes B from 2-25', and the herbaceous and other cover H less than 2' from the ground. And the sequence of patches encountered in moving through the habitat (or in taking ever larger samples) is then represented by a sequence of letters *e.g.* C, B, H, H, B, C, . . ., with certain random properties but also subject to the condition that the long term frequency of C's, B's, and H's should conform to their respective densities (p_i) in the particular habitat. If the sequence is ergodic, which defines what we call a homogeneous habitat, then it is well known that the uncertainty of the next letters in the sequence is appropriately measured by the formula $-\sum_i p_i \log_e p_i$ which we used. If, instead of considering

the uncertainty of future single letters in the sequence, we ask for the uncertainty of future pairs of letters, the formula becomes $-2 \sum_i p_i \log_e p_i$ which is $2 \times$ foliage

height diversity, which is essentially the predicted value of the bird species diversity. Thus we can say that bird species diversity is determined as if the birds recognized suitable habitats by pairs of foliage types ($> 25'$, $2-25'$, $0-2'$). The species area curve could then be predicted from this.

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aspects of this research at length and it has benefited from their ideas. James Preer helped make the measurements.

SUMMARY

1. Bird censuses on a wide variety of areas are compared in order to see what aspects of environmental variation control bird species diversity.
2. Indeciduous forests, bird species diversity can be predicted in terms of the height profile of foliage density. Plant species diversity, except by influencing this profile, has nothing to do with bird species diversity. The layers 0-2', 2'-25', > 25' seem equally important in determining bird species diversity; these layers presumably correspond to different configurations of foliage. This should not be interpreted as evidence that a forest is made up of discrete layers. These 3 layers are constructed by the observer.
3. An evolutionary argument is given which predicts the observations and at the same time suggests that niches should be "convex." Supporting evidence is provided.
4. These results provide no evidence about the real causes of tropical diversity (*i.e.* whether the temperate regions, given enough time, can support as great a diversity as the tropics now have) or about the diversity which could be expected in a composite census of 2 habitats. These are essentially different problems and are under investigation now.

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HABITAT OF JUVENILE SHRIMP (FAMILY PENAEIDAE)¹

GORDON GUNTER²

Texas Game and Fish Commission, Field Laboratory, Seabrook, Texas

For the past 50 years penaeid shrimp have been studied along the shores of the Gulf of Mexico and the South Atlantic coast of the United States. These shrimp are of intrinsic interest to zoologists. The group differs from

¹Contribution No. 53 from the Marine Laboratory, Texas Game and Fish Commission.

²Present address, Gulf Coast Research Laboratory, Ocean Springs, Mississippi.

other higher Crustacea in that the eggs are shed free into the water and develop into larval stages ranging from nauplii (very similar to early copepod developmental stages) to post-larvae, with as many as 14 probable molts intervening, the precise number still being a matter of argument. A 2nd reason for the extensive study of the Penaeidae is that the shrimp fishery is the most valuable one in the United States (*cf.* the various annual fishery