reaching the sea during spring freshets, to be carried well offshore, become waterlogged, and sink to the bottom

According to Jannasch *et al.* (*14*) microbial decomposers, other than those which may occur in the gut of invertebrates (*15*), exhibit little activity at great depths, and Kohlmeyer (*16*) reports the same for fungi. The Xylophagainae utilize wood both as a substrate and for food (either as host organisms for symbiotic bacteria in the gut or by means of an endogenous cellulase). It is now apparent that they are the most important deep-sea organisms involved in converting woody plant material to available food sources (i) in the form of fecal pellets for detritus feeders, (ii) as larvae or adults, exposed by the disintegration of the wood, for predators, and (iii) as dead remains for scavengers.

High population densities, high reproductive rates (*17*), early maturity, rapid growth, apparent ease of dispersal, and the ability to utilize a transient habitat make these wood borers classic examples of opportunistic species (*18*), the first recorded for the deep sea.

It has been noted that dredge hauls rich in terrestrial plant material also contain a great variety of animals (*19–21*), indicating that a patchy, uneven distribution develops around islands of such material. Wood carried far out to sea and sinking at scattered points is relatively transient and favors opportunistic species. In deep water off the mouths of rivers, off swampy or wooded coastlines, and in trenches, wood is a more common feature of the bottom (*21*) and produces a continuing patchy environment. These more persistent but constantly shifting "islands" allow for the development of opportunistic species, serve as dispersal centers from which larvae emanate to settle on isolated islands, and contribute to habitat diversity, niche specialization, and enrichment.

The arrival of wood on the bottom may be thought of as a "predictable disturbance" in the sense of Dayton and Hessler (*22*), the role of the borers as decomposers of the wood being comparable to that of the "croppers" in utilizing and distributing the animal remains. The predictability of the arrival of wood on the bottom allowed for the evolution of the Xylophagainae, while the unpredictability of the point of arrival led to their opportunism. Such disturbances do not detract from the stability-time hypothesis proposed by Sanders (*23*) to explain diversity in the deep sea. Rather, they add factors

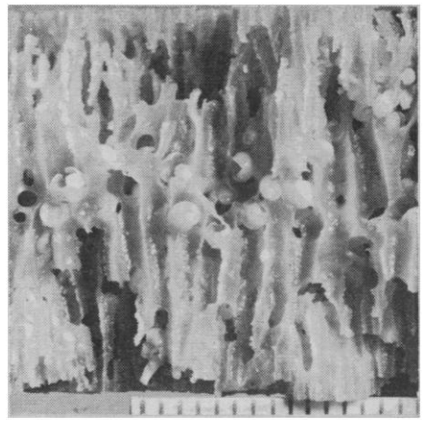

Fig. 3. Section through the panel in Fig. 2, showing burrows entering from both sides, the specimens meeting in the middle. (The scale is marked in millimeters.)

contributing to diversity without altering the present view of the abyss as a predictable environment.

The validity of these ideas can be tested by (i) analyzing the effects of introducing islands of woody plant material and (ii) dredging and submersible programs designed to look at the quantity and distribution of land plant material in the deep sea in conjunction with a study of river effluents and ocean currents.

RUTH D. TURNER
Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138

References and Notes

1. The D.S.R.V. *Alvin* is a small deep-sea submersible operated by Woods Hole Oceanographic Institution.
2. The values of the largest *Xylophaga* in the wood were 1.5 mm long, while those of specimens taken from a larger, thicker piece of wood dredged in the same general area were 7.5 mm long.
3. R. D. Purchon, *J. Mar. Biol. Ass. U.K.* **25**, 17 (1941).
4. R. D. Turner, in *Marine Borers, Fungi and Fouling Organisms of Wood*, G. Jones and S. Eltringham, Eds. (Organization of Economic Cooperation and Development, Paris, 1971), p. 269.
5. ———, in *Holz und Organismen*, G. Becker and W. Liese, Eds. (Duncker & Humblot, Berlin, 1966), pp. 441–445.
6. J. S. Muraoka, *Deep-Ocean Biodeterioration of Materials*, part 4, *One Year at 6,800 Feet* (Technical Report R 456, U.S. Navy Civil Engineering Laboratory, Port Hueneme, Calif., 1966), pp. 18–24.
7. R. Tipper, thesis, Oregon State University (1968).
8. P. Wiebe, Woods Hole Oceanographic Institution, used a Longhurst-Hardy plankton recorder with a mesh size of 0.333 mm. The recorder was attached to the *Alvin* and held 10 cm off the bottom while the ship moved at 1 knot (1.85 km/hour).
9. Estimates of growth rates are based on laboratory culturing of other species and on test panels exposed in other areas (*4, 6, 7*).
10. R. Y. George and R. J. Menzies, *Nature* **215**, 878 (1967).
11. A. Schoener, *Ecology* **49**, 81 (1968).
12. H. L. Sanders and R. R. Hessler, *Science* **163**, 142 (1969).
13. P. J. Darlington, *Zoogeography* (Wiley, New York, 1957), pp. 15–17.
14. H. W. Jannasch, K. Eimhjellen, C. O. Wirsen, A. Farmanfarmaian, *Science* **171**, 672 (1971).
15. H. W. Jannasch and C. O. Wirsen, *ibid.*, in press.
16. J. Kohlmeyer, *Amer. Soc. Test. Mater. Spec. Tech. Publ. No. 445* (1969), pp. 20–30.
17. An estimate of egg numbers based on histological study of the gonads is about 30,000.
18. R. MacArthur, *Amer. Natur.* **44**, 25 (1960); J. S. Levinton, *Lethaia* **3**, 69 (1970).
19. A. Agassiz, *Three Cruises of the Blake* (Houghton Mifflin, Riverside Press, Cambridge, Mass., 1888), vol. 1, p. 291; A. Bruun, *Geol. Soc. Amer. Mem. 67* (1957), vol. 1, p. 650.
20. T. Mortenson, *Annot. Zool. Jap.* **17**, 225 (1938).
21. A. Bruun, *Galathea Rep.* **1**, 15 (1959).
22. P. K. Dayton and R. R. Hessler, *Deep-Sea Res.* **19**, 199 (1972).
23. H. L. Sanders, *Amer. Natur.* **102**, 243 (1968).
24. A. S. Jensen, *Dan. Ingolf-Exped.* **2** (No. 5), 56 (1912).
25. J. Knudsen, *Galathea Rep.* **5**, 163 (1961).
26. J. Thiele and S. Jaeckel, *Wiss. Ergeb. Deut. Tiefsee-Exped. "Valdivia"* **21** (No. 1), 159 (1931).
27. M. Weber, *Siboga Exped.* **1**, 1 (1902).
28. R. D. Turner, personal observation.
29. L. Barnard, *Galathea Rep.* **5**, 23 (1961).
30. H. Milne-Edwards, *Bull. Mus. Comp. Zool. Harvard Univ.* **8**, 38 (1880); A. Agassiz, *Three Cruises of the Blake* (Houghton Mifflin, Riverside Press, Cambridge, Mass., 1888), vol. 2, p. 40.
31. T. Wloff, *Galathea Rep.* **6**, 233 (1962).
32. J. B. Kirkegaard, *ibid.* **2**, 63 (1956).
33. Identified by M. Rice (National Museum of Natural History, Smithsonian Institution).
34. Thanks are extended to H. Sanders, F. Grassle, A. Schoener, J. Jannasch, K. J. Boss and M. Rex for reading the manuscript, and to A. Coleman for photographic work. Contribution No. 3047, Woods Hole Oceanographic Institution. Supported by ONR contract NOOO 14-67A-0298-0027 with Harvard University and NSF grant GD-32558 to Woods Hole Oceanographic Institution.

20 February 1973

Succession: Similarities of Species Turnover Rates

Abstract. *The rate coefficients for species turnover (the proportion of species lost per unit time) for successional communities decrease as the communities approach some equilibrium state. This observation makes it possible to determine the parameters of a two-parameter model which quantifies the time variation of successional changes in the second derivative.*

Several investigators (*1*) have noted common features of ecological succession (the orderly progression of ecological communities through time); for example, species diversity, structural complexity, biomass, and perhaps stability commonly tend to increase with the successional age (time since perturbation) of an ecosystem. We examined the rate coefficients for species turnover in published studies on succession (*2*) to associate community dynamics

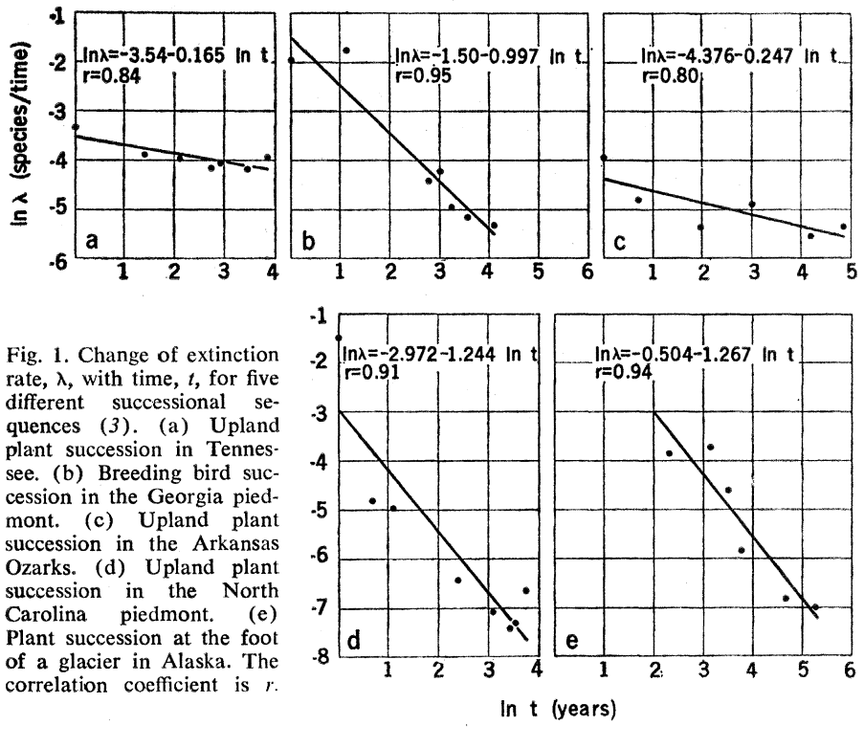

Fig. 1. Change of extinction rate, λ, with time, t, for five different successional sequences (*3*). (a) Upland plant succession in Tennessee. (b) Breeding bird succession in the Georgia piedmont. (c) Upland plant succession in the Arkansas Ozarks. (d) Upland plant succession in the North Carolina piedmont. (e) Plant succession at the foot of a glacier in Alaska. The correlation coefficient is r.

with succession. Species turnover rate is defined as the number of species lost from a community per unit time, and the rate coefficient is derived from the model

$$L = \lambda S \qquad (1)$$

where L is the species turnover rate, S is the number of species in a community, and λ is the rate coefficient. The species turnover rate is a term of a general model,

$$\frac{dS}{dt} = I - L \qquad (2)$$

where I is the input or colonization rate of new species into the community and t is time. In a dynamic system operating as indicated in Eqs. 1 and 2, one can solve for λ by the formula

$$S(t) = S(0)e^{\lambda t}$$

where $S(0)$ is the number of species present at some time zero and $S(t)$ is the number of the same species remaining at some time t. We solved for λ by using linear regression with a logarithmic transformation on the dependent variable. By calculating a λ value for each of the communities in a successional sequence it is possible to determine the change in λ with the age of the seral communities.

For all communities examined, λ was found to decrease with the age of the community, which indicates a deceleration in the rate of species loss. This pattern applies to heterotrophic and autotrophic successions, aquatic and terrestrial successions, and successions in laboratory microcosms and large natural ecosystems. Since species turnover can be applied to quite different communities, it is a usable index for comparative studies on successional systems.

Figure 1 shows the species turnover rate coefficients plotted as a function of time (age of the community in the successional sequence). In these five examples the dependent variable, λ, and the independent variable, t, are both in logarithmic form. A logarithmic transformation on the time axis seems appropriate in that field investigators typically sample successional sequences according to a quasi-logarithmic sampling scheme (for example, communities might be sampled at 1, 2, 5, 10, 17, 35, 60, and 100 years). By using regression to fit the time-varying nature of λ, a two-parameter expression for the loss of species is provided, namely

$$\log(\lambda) = b \log(t) + \log(a)$$

or

$$\lambda = at^b$$

where a and b are model parameters which can be used to quantify successional dynamics. In all examples (Fig. 1) b is negative, indicating that species loss decelerates with time. Since λ is fitted by a power function of time, this deceleration is most pronounced early in the successional sequence. The parameter a quantifies the initial velocity (turnover rate) of species loss.

In Fig. 1, b, d, and e, the slopes are similar but the a values are quite different. This indicates that, although the decelerations appear to be similar, the species turnover rates differ considerably. In forest succession in Alaska (Fig. 1e) species are retained for a longer period of time than in forest succession in North Carolina (Fig. 1d). Species in a bird community in Georgia (Fig. 1b) turn over more slowly than plant species in a piedmont community in North Carolina (Fig. 1d).

In the other examples, the slopes in Fig. 1a (forest succession in the central basin of Tennessee) and Fig. 1c (forest succession in the Ozark plateau of Arkansas) are rather similar and differ significantly ($P \geq .95$) from the slopes in Fig. 1, b, d, and e. Since the values of b for mesic successions (Fig. 1, b, d, and e) are similar to one another but significantly different from those for xeric successions (Fig. 1, a and c), one might infer that this parameter is determined by local site conditions, whereas parameter a tends to vary geographically. In Fig. 1, mesic successions have values of b ranging from -0.997 to -1.267, whereas xeric successions have much higher b values (-0.165 and -0.242), which indicates that λ decreases more rapidly in mesic successions. For plant communities in Fig. 1, parameter a (the initial rate coefficient for species loss) is largest in the study in Alaska (-0.504) and is considerably lower (-2.972 to -4.376) in studies conducted in the southern United States. More complete data sets need to be developed for the determination of factors that influence the magnitude of a and b and for comparative studies of turnover rates of different functional groups (such as the comparison between turnover rates for bird and plant species in Fig. 1, b and d).

Through landscape manipulation man is altering successional rates. The magnitude of these effects is not known and only quantification of natural processes will provide the base data needed for comparison. Determination of dynamic successional parameters such as a and b is imperative for the construction and subsequent utilization of regional forest succession models.

HERMAN H. SHUGART
JOAN M. HETT*
Environmental Sciences Division,
Oak Ridge National Laboratory,
Oak Ridge, Tennessee 37830

References and Notes

1. F. B. Golley and J. B. Gentry, *Oikos* **15**, 185 (1966); R. Margalef, *Perspectives in Ecological Theory* (Univ. of Chicago Press, Chicago, 1968); C. D. Monk, *Amer. Natur.* **101**, 173 (1967); E. P. Odum, *Science* **164**, 262 (1969); E. C. Pielou, *J. Theor. Biol.* **10**, 370 (1966); R. H. Whittaker, *Science* **147**, 250 (1965).
2. Over 200 publications were examined. The references were drawn from P. T. Haug and G. M. Van Dyne, *Secondary Succession in Abandoned Cultivated Fields: An Annotated Bibliography* (Publ. No. 228, Ecological Sciences Division, Oak Ridge National Laboratory, Oak Ridge, Tenn., 1968); P. T. Haug, thesis, Colorado State University (1970). Most of the sources did not contain sufficient information for us to calculate species turnover rate coefficients as a function of time.
3. The sources of the data used in Fig. 1 are: (a) D. W. Smith, thesis, University of Tennessee (1968); (b) D. W. Johnston and E. P. Odum, *Ecology* **37**, 50 (1956); (c) H. H. Shugart, thesis, University of Arkansas (1968); (d) H. H. Oosting, *Amer. Midl. Natur.* **28**, 1 (1913); and (e) W. A. Reiners, I. A. Worley, D. B. Lawrence, *Ecology* **52**, 55 (1971).

4. Supported by the Eastern Deciduous Forest Biome Project, International Biological Program, funded by the National Science Foundation under interagency agreement AG-199, 40-193-69 with the Atomic Energy Commission–Oak Ridge National Laboratory. Oak Ridge National Laboratory is operated by Union Carbide Corporation for the U.S. Atomic Energy Commission. Contribution No. 82 from the Eastern Deciduous Forest Biome.

* Present address: Coniferous Forest Biome, International Biological Program, Oregon State University, Corvallis 97331.

15 January 1973

Testosterone Concentration in the Male Chick Brain: An Autoradiographic Survey

Abstract. *Differential uptake of [^{3}H]testosterone in male chick brain was found in periventricular areas of preoptic-hypothalamic continuum. Concentration of silver grains for all decapitation periods was especially high in the medial preoptic area, particularly the nucleus praeopticus paraventricularis magnocellularis. Distribution of testosterone-sensitive cells is in agreement with studies showing neuroanatomical control of reproductive behavior by the avian forebrain.*

Recent studies using the domestic chick have shown the preoptic-anterior hypothalamic continuum to be involved in patterns of reproductive behavior. Specifically, precocial copulation in the male chick has been activated by testosterone implants in the preoptic region (*1*), inhibited by progesterone implants placed in the medial preoptic area (*2*), and disrupted through bilateral electrolytic lesions in the anterior hypothalamus (*3*). These data suggest that hormone-sensitive neurons exist in the male chick brain, possibly similar in neuroanatomical distribution to the male rat, where autoradiographic surveys have shown the presence of androgen-sensitive (*4*) and estrogen-sensitive (*5*) neurons.

The purpose of the present study was to determine the topographical distribution of androgen-sensitive cells in the male chick brain by surveying for the differential uptake of tritiated testosterone. The autoradiographic technique has been a useful method for mapping hormone-sensitive sites in the mammalian brain (*4*, *5*), and recent studies (*6*) have incorporated improvements in order to minimize artifactual data due to diffusion of water-soluble compounds. In the present study, brain tissue was sliced in a microtome-cryostat under safelight and directly mounted on slides precoated with photographic emulsion. The resultant autoradiograms contained adequate cellular resolution for the analysis of silver grain concentrations in various neuroanatomical areas.

Fifteen male Rhode Island Red × White Rock chicks were reared in isolation. At 2 weeks of age, they were subcutaneously injected with 200 μc (1.3 μg) of 1,2-[^{3}H]testosterone (specific activity 45 c/mmole), and decapitated ½ hour ($n = 3$), 2 hours ($n = 4$), or 3 hours ($n = 5$) later. One chick for each of the three decapitation times was injected with unlabeled testosterone. Brains were removed after decapitation and frozen in powdered CO_2. Brain tissue was sliced at 6 μm in a cryostat at −18°C, under safelight conditions (*7*), and the sections were mounted directly on slides precoated with emulsion (Kodak NTB-3). The slides were then packed in lightproof boxes, placed in plastic containers under partial vacuum, and exposed in lead-lined boxes at 5°C. After an exposure period of 4 to 6 months, the autoradiograms were developed and stained with thionin.

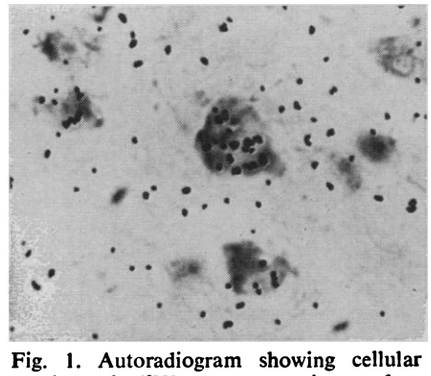

Fig. 1. Autoradiogram showing cellular uptake of [^{3}H]testosterone in nucleus praeopticus paraventricularis magnocellularis (× 450). Exposure 146 days, 3-hour decapitation.

Quantitative analyses of reduced grains beneath brain cells were performed for each of the 18 neuroanatomical areas (*8*) given in Table 1. Fifty cells were counted under bright-field microscopy at × 400 for each brain area in every animal. Radioactivity beneath cell bodies for the three decapitation times is given in Table 1. These data, grouped according to neuroanatomical area, are presented in terms of mean grains per cell body, and also as the mean number of labeled cells, that is, cells which contained 11 or more silver grains. Highest mean uptake over the three decapitation periods was seen in the nucleus praeopticus paraventricularis magnocellularis, which consistently showed the greatest mean concentration of reduced grains per cell, as well as cells with 11 or more grains. In addition, relatively high mean grain counts were found in the nucleus supraopticus, nucleus praeopticus medialis, nucleus hypothalamicus anterior medialis, nucleus paraventricularis magnocellularis, and nucleus hypothalamicus posterior medialis. A labeled neuron in the nucleus praeopticus paraventricularis magnocellularis is shown in Fig. 1.

Generally, reduced grain content decreased as decapitation time increased, although the nucleus praeopticus paraventricularis magnocellularis retained high mean grain counts for all three decapitation periods. Chicks injected with unlabeled testosterone had low concentrations of silver grains throughout the brain, and averaged no higher than 1.03 ± 0.37 grains per cell in any neuroanatomical area. In no instance did an unlabeled control contain a cell with 11 or more grains. Moreover, experimental slides which had been fogged with light showed no fading of the latent image.

In order to determine the highest uptake over the three decapitation times, the chi-square test was used to compare neuroanatomical areas for differences between labeled (11 or more grains) and unlabeled cells. The nucleus praeopticus paraventricularis magnocellularis had scores for mean labeled cells which were higher than all other areas within the 2- and 3-hour decapitation periods ($P < .05$),