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This review deals with annual production by the freshwater animal groups: fishes, zoobenthos, and zooplankton. Included are the concept and terminology of productivity, methods for estimating annual production, the production/biomass ratio, and levels of production by the three groups from the world literature. [The SC¹® indicates that this paper has been cited in over 180 publications.]

Animal Production in Fresh Waters

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In 1974, Professor Amyan Macfadyen, editor of *Advances in Ecological Research*, wrote to me and suggested a review of "secondary production measurement." I immediately agreed because, at that date, the subject of freshwater production had been researched with some intensity for the past decade, and the first major accumulation of data had been done. The time seemed particularly opportune to critically summarize methods, which had reached a point of soundness and broad applicability, and to collect into one place most of the world's production data. Another objective was to clarify the concept and terminology of production, at that time in a bit of a mess in the literature. I felt it would be helpful to also convert the mélange of units in the literature into a single expression for each of the three major groups: kg/ha/yr (wet) for fish, kg/ha/yr (dry) for zoobenthos, and g/m²/yr (dry) for zooplankton.

The definitive beginning of aquatic production literature is usually credited to the paper of P. Boysen-Jensen¹ on a marine benthos.

But the first great stimulation, conceptually and mathematically sound, was that presented independently by W.E. Ricker² and K.R. Allen³—what we now call the instantaneous growth rate (IGR) method for estimating fish production. Even so, a long lag occurred between the mid-1940s and important further advances; H.B.N. Hynes⁴, in reviewing stream ecology literature through 1966, considered production research to be in its infancy. By about the mid-1960s, however, the International Biological Program (IBP), emphasizing productivity, had given great impetus to research on the subject, and a few landmark papers had also appeared by that time. Furthermore, a methodological breakthrough for benthos production was presented by Hynes⁵ that now, after further development, we term the size-frequency method.

By the mid-1970s, then, a viable, decade-long literature had accumulated. Thus, I think the reason for the frequent citation is that my review served as a linchpin for further work, appropriately located in time. Subsequent authors could refer to the definition of production without giving a complicated explanation of their own; the methods were given in a somewhat recipe-book style and could be readily referenced; and the literature data, summarized in tabular form with common units, could be easily examined.

No comparable review has been subsequently published, although A.C. Benke⁶ reviewed in depth the concept and methods for benthos, and R.H.K. Mann and T. Penczak⁷ summarized production by river fishes. The revised IBP handbook on secondary productivity in fresh waters deals with a number of related subjects.⁸

During the most recent decade, a large number of additional estimates have been published, particularly on fishes and stream benthos. Methods used are basically the same but have been fine-tuned in some critical respects. Methods used today most commonly appear to be the IGR method for fish and the size-frequency method for benthos.

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2. Ricker W E. Production and utilization of fish populations. *Ecol. Monogr.* 16:373-91, 1946. (Cited 145 times.)
3. Allen K R. Some aspects of the production and cropping of fresh waters. *Trans. Roy. Soc. N. Z.* 77:222-8, 1949. (Cited 20 times.)
4. Hynes H B N. *The ecology of running waters*. Liverpool, England: Liverpool University Press, (1970) 1982. 580 p. (Cited 745 times.)
5. ———. The invertebrate fauna of a Welsh mountain stream. *Arch. Hydrobiol.* 57:344-88, 1961. (Cited 220 times.)
[See also: Hynes H B N. Citation Classic. (Barrett J T, comp.) *Contemporary classics in plant, animal, and environmental sciences*. Philadelphia: ISI Press, 1986. p. 164.]
6. Benke A C. Secondary production of aquatic insects. (Resh V H & Rosenberg D M, eds.) *The ecology of aquatic insects*. New York: Praeger, 1984. p. 289-322. (Cited 20 times.)
7. Mann R H K & Penczak T. Fish production in rivers: a review. *Polish Arch. Hydrobiol.* 33:233-47, 1986.
8. Downing J A & Rigler F H, eds. *A manual on methods for the assessment of secondary productivity in fresh waters*. Oxford, England: Blackwell Scientific, 1984. 501 p.