Ricker W E. Stock and recruitment. *J. Fish. Res. Board Can.* **11**:559-623, 1954.
[Pacific Biological Station, Nanaimo, British Columbia, Canada]

A life-history mechanism is demonstrated whereby cycles of abundance can be generated independently of any environmental cycle. In multi-aged stocks, their period is equal to twice the mean interval from parental to progeny reproduction. [The *SCI*® indicates that this paper has been cited over 165 times since 1961.]

W.E. Ricker
Pacific Biological Station
Department of Fisheries and Oceans
Nanaimo, British Columbia V9R 5K6
Canada

February 24, 1982

"During the 1930s, A.J. Nicholson[1] developed the thesis that the abundance of an organism had to be limited by a *compensatory* mechanism—one that reduced reproduction or survival rate when abundance exceeded some limit, and allowed it to increase when below that limit. This 'blinding glimpse of the obvious' started me thinking about its possible consequences for fish populations. At that time, most fishery biologists faced with this problem would, either overtly or tacitly, take one of two extreme positions: either they assumed that an increase in parent stock would tend to produce a proportional increase in recruitment to the stock, or they assumed that recruitment always tended to be at its maximum level regardless of any conceivable fluctuation in the abundance of spawners. Both schools, of course, allowed that a variable environment could change the number of recruits actually obtained from any year-class.

"From the Nicholsonian point of view these two extremes had to be connected by intermediate situations, so I drew a series of curves representing the various possibilities. Central to all such curves of recruits versus parents is a *replacement line*, where recruitment would maintain the stock at its then level, and a *replacement point*, where mean recruitment was in fact just sufficient for maintenance. Some portion of each curve had to lie above the replacement line, but apart from that, quite varied shapes were theoretically possible, and maximum recruitment could occur when spawners were either more or less numerous than the replacement level. In the latter case, the curve generated oscillations in abundance. These were damped if the curve crossed the replacement line with a slope less than 45°, but permanent if the slope was greater. A number of examples were found, both natural and experimental, of population oscillations that could be interpreted in this manner. For populations containing adults of more than one age it was shown that: (1) oscillations were increasingly likely, the longer the period of immaturity; (2) the period of such oscillations was equal to twice the interval from parental reproduction to the median time of reproduction of their progeny; and (3) harvesting part of a stock reduced the period and amplitude of the oscillations and could destroy them entirely.

"Fishery biologists may cite this paper mainly because of its appendix. This develops an expression which, I found to my surprise, can describe a large fraction of observed recruitment curves. It is now usually written $R = aPe^{-bP}$ (R, recruitment; P, spawners; a and b, parameters). It implies that the rate of compensatory mortality of immatures is proportional to their abundance at the *start* of the compensatory phase.

"Looking back, I can't help but reflect that the extensive trial computations, done over a period of several years, that were the basis of this paper could be done today in less than one-tenth the time, using a $25 hand computer. But could my ideas have kept pace? I'm inclined to doubt it.

"The recruitment problem attracted increasing attention during the 1960s following the collapse of several major fisheries, so that in 1970 a symposium in Denmark attracted 42 contributions."[2]

1. **Nicholson A J.** The balance of animal populations. *J. Anim. Ecol.* **2**:132-78, 1933.
2. **Parrish B B,** ed. Proceedings of a symposium on fish stocks and recruitment, Aarhus, Denmark, 7-10 July 1970. (whole issue.) *Rapports Procès-verbaux Conseil Int. Explor. Mer* **164**, 1973. 372 p.