Rethinking Stock Recruitment: In memoriam to Bill Ricker

SYMPOSIUM PROCEEDINGS

Dick Beamish
Brian Riddell
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International Congress on the Biology of Fish

University of British Columbia, Vancouver, CANADA

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Don MacKinlay
Congress Chair

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WILLIAM EDWIN RICKER OC, FRSC, LLD, DSc.

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In 1973, Bill Ricker retired at age 65 from his responsibilities with the Fisheries Research Board of Canada. He had worked 27 years for the "Board", 11 years at Indiana University, and one year at the International Pacific Salmon Commission. Over this period and through to his death on the 8th of September, 2001, he produced an amazing array of scientific publications that improved our understanding of nature and helped to found a science needed to manage the developing world fisheries.

It is difficult to know Bill Ricker. With considerable work, it is possible to identify his many and varied scientific accomplishments. It is more difficult to measure the influence he had on an entire generation of scientists. As an intently private individual, it is especially hard to understand Bill on a personal level. Discussions with his sons and grandchildren produce an understanding of his love for his wife Marion who predeceased him and of his devotion to his children and their interests.

Bill had a partiality towards young people all his life and this kept him young at heart. He particularly enjoyed being part of the adventures of his sons and their friends, which caused Bill to be very active in the Scouting movement in the 1950s. It seems that this spirit of adventure combined with a love of nature guided a young Bill Ricker into a life of discovery.

Bill Ricker's life is an inspiration to any young biologist contemplating a career in aquatic sciences. Few could hope to make as many contributions, but most could learn from his approach to science. He knew the scientific literature, no matter where it was published. He was clear about his assumptions. He was meticulous and applied good common sense and sound logic. He developed his concepts using simple examples. But most importantly, he communicated the results of his studies to his colleagues. A compilation of his publication includes 296 published papers and books, 238 published translations, and 148 scientific or literary manuscripts (K. Ricker 1998; customercare@accutype.net). Included in this total were 38 papers on stoneflies, describing 88 new species. To Bill, every day was a good day to discover something new.

In fisheries, Bill Ricker focused on issues that were vitally important to Canada's commercial fisheries and to the science needed to manage them. However, he also found time to become a world authority in the taxonomy of stoneflies. In fact, it has been noted that some scientists believed that there were two W.E. Rickers as the contribution of the entomologist W.E. Ricker was exceptional for any one person. Bill Ricker described 81 of the total of 617 stoneflies now listed in North America. His interests in stoneflies extended into their zoogeography and evolution. Bill recognised distinctions within accepted genera, which he partitioned into subgenera in his classifications. These subgenera were later considered to be distinct genera. In fact, about one-third of the 101 genera currently recognised in North America were originally identified by Bill Ricker. Fellow entomologists wrote that his system of classification was "a thing of beauty and simplicity that made evolutionary sense".

In fisheries he is best known for his 1954 paper on "Stock and Recruitment" and his "Handbook of Computation for Biological Statistics of Fish Populations", first published in 1958. There were 36 of his own papers referenced in the 348-page handbook. His handbook became the standard reference for students and professionals around the world. It is still used in China as the standard text for Fisheries Science. Bill was appointed editor of the Journal of the Fisheries Research Board in 1950, and during his 11 or 12 year tenure he turned what was a parochial journal into perhaps the world's most influential fisheries science publication. He was a meticulous, but supportive editor. The credibility of the journal was so universal that having a paper accepted was a mark of accomplishment, even before the content was read. It is important to put Bill Ricker's life into perspective. He had one assistant as editor and he did not have other staff to help him collect, store, retrieve, and analyse data.

Bill was aware of the accomplishments of the famous Russian fisheries scientist, Feodor Baranov. Bill taught himself Russian while at Indiana University so that he could read Baranov's original papers. He created an awareness of Russian fishery science in the English speaking community through his published translations and his 428 page Russian-English Dictionary on terminology in hydrobiological science for students of Fisheries and Aquatic Biology. This dictionary remains the only specialised text on fisheries terminology.

He received about 27 medals and awards including the Flavelle Medal (1970), the Professional Institute of the Public Service of Canada Gold Medal (1966) and the F.E.J. Fry Medal (1983). In 1969, he was honoured by the American Fisheries Society for his superb and original contributions to fisheries science and received their first Award of Excellence. The society later established the William E. Ricker Resource Conservation Award, which was given to the Pacific Biological Station in 2001. It was a recognition that greatly pleased Bill. Dr. Bill Ricker received honorary doctoral degrees from the University of Manitoba, Dalhousie University and the University of Guelph. The recognition he particularly cherished was the naming of the Canadian Fisheries Research Vessel, the W.E. Ricker in 1986, the same year he was appointed to the Order of Canada.

Bill Ricker was an unassuming, gentle, humble man. Through his pervasive curiosity and his ability to retain knowledge, he charted a course for fisheries science that opened areas for discovery all around the planet. This was Bill's gift to the young and young at heart. He will be missed but never forgotten.

Bill Ricker on the Canadian research vessel named after him in 1986 with his granddaughter Andrea wearing his order of Canada, which he also received in 1986.

CURIOSITY, BIFURCATION AND CHAOS:

A TRIBUTE TO BILL RICKER'S INQUIRING MIND

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EXTENDED ABSTRACT ONLY – DO NOT CITE

Bill Ricker retired from his position as scientist at the Pacific Biological Station in Nanaimo, British Columbia, three years before I began working there. Because he retained an office and used it frequently, I didn't realize at first that he was, in fact, retired. Although I knew of his reputation as an accomplished scientist, it took me many years to appreciate the scope of his achievements. I began working in fisheries as a naïve mathematician, with much to learn about biology and the broader world of scientific inquiry. Bill brought a compelling curiosity to any subject that interested him. For example, he introduced me to the controversies about crop circles with the investigative article by Nickell and Fischer (1992).

As a mathematician, I had the opportunity to participate in some of Bill's mathematical recreations. He would occasionally pass me articles of interest, such as Stewart's (1995) discussion of flower structures. What algorithm could possibly explain the beautifully tight packing of seeds on the head of a sunflower? A possible answer relates to:

- the Fibonacci sequence 1, 1, 2, 3, 5, 8, 13, 21, 34,…, in which each number is the sum of the previous two,
- the golden number $\varphi = \frac{\sqrt{5}-1}{2}$ defined by the equal ratios $\frac{\varphi}{1} = \frac{1}{1+\varphi}$, and
- the golden angle $\theta = (1-\varphi)\times 360^\circ = 137.507764\cdots^\circ$.

Successive Fibonacci ratios tend to the golden number, that is $\frac{1}{1}, \frac{1}{2}, \frac{2}{3}, \frac{3}{5}, \frac{5}{8}, \frac{8}{13}, \frac{13}{21}, \frac{21}{34}, \cdots \to \varphi$, and the golden angle helps define the packing algorithm. To draw n points (x_k, y_k) within the unit circle, use the formulas

(1) $$x_k = \sqrt{k/n}\cos(k\theta),\ y_k = \sqrt{k/n}\sin(k\theta),\ \text{where } k = 1,\ldots,n.$$

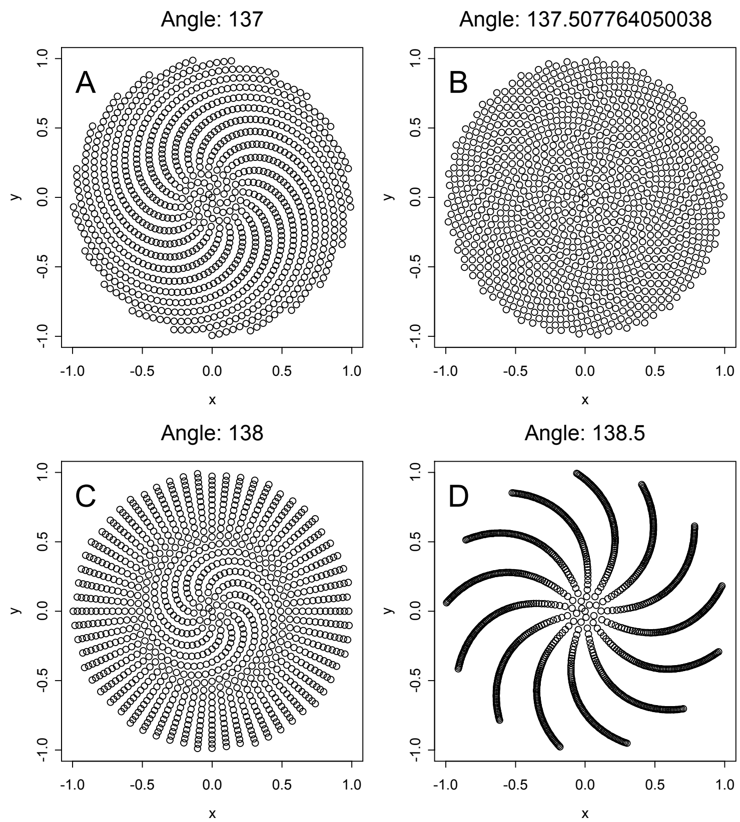

Figure 1. Patterns of $n = 1000$ points (x, y) produced by the algorithm (1) with various rotational angles θ. In panel B, θ is the golden angle $(1-\varphi)\times 360^{\circ}$.

In polar coordinates, each successive point is located by rotating through the angle θ and increasing the distance from the origin slightly, where the square root gives a radial distance that produces even spacing of points within the area. Figure 1B shows the outcome of the algorithm (1) with the golden angle θ. Nearby angles θ gives distinctly different results in Figs. 1A, 1C, and 1D. This example illustrates two important features of a chaotic process:

- a simple algorithm can produce a complex pattern, and
- a small change in the algorithm can produce a major change in the pattern.

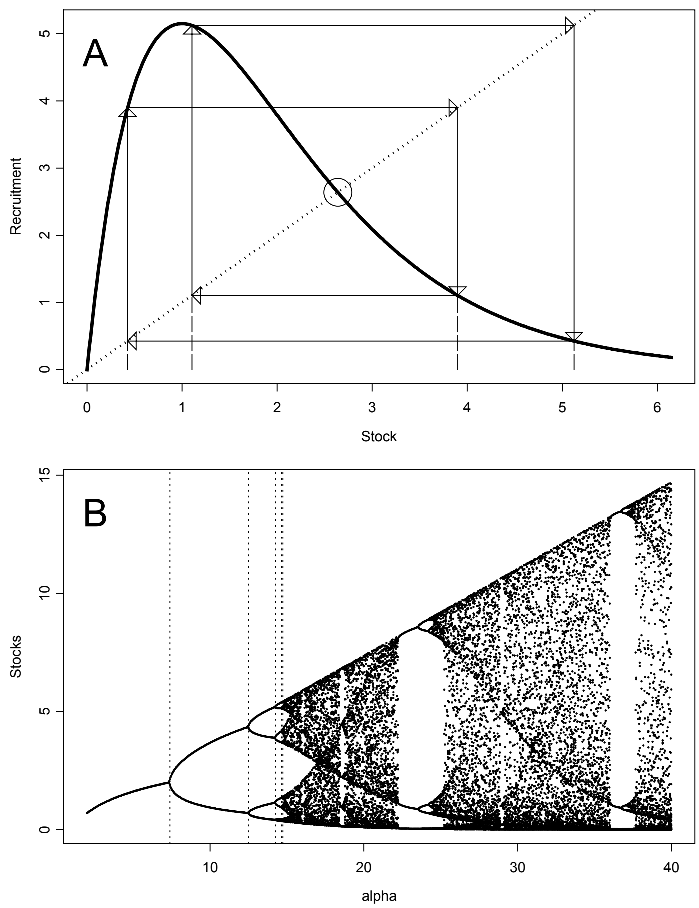

Figure 2. (A) Ricker curve with $\alpha = 14$ and $\beta = 1$ (thick solid line), showing the stable oscillating pattern among four stock sizes. Arrows indicate the progression from a stock S to a recruitment R and then to the next stock S, via the line $R = S$ (dotted). A circle marks the replacement point (2), which is not stable in this case. (B) Stable stock sizes in relation to α for a Ricker curve with $\beta = 1$. The initial line segment on the left corresponds to the single equilibrium value S_{eq} in (2) for $\alpha \le \alpha_1$.

Ricker's famous curve $R = \alpha S e^{-\beta S}$, which describes the relationship between stock S and subsequent recruitment R, also has interesting chaotic properties. In 1995, Bill asked me why his curve appeared as an example in a technical book by a Russian author (Kuznetsov 1995, p. 112). The answer relates to stable points in the implied population dynamics. If the stock replaces itself in each generation $(R = S)$, then Ricker's equation becomes $S = \alpha S e^{-\beta S}$, with the equilibrium solution

(2) $$S_{\text{eq}} = \frac{1}{\beta} \log \alpha .$$

In fact, this simple result fails to capture complex behaviour of the Ricker function, which depends on critical values of the parameter α given by

(3) $$\alpha_1 = e^2 = 7.38907\cdots, \ \alpha_2 = 12.50925\cdots, \ \alpha_3 = 14.24425\cdots, \ \alpha_4 = 14.65267\cdots, \ \ldots .$$

The equilibrium value S_{eq} in (2) becomes unstable when $\alpha > \alpha_1$. The stock alternates between two equilibrium sizes when $\alpha_1 < \alpha \le \alpha_2$, and more generally oscillates through 2^k sizes when $\alpha_k < \alpha \le \alpha_{k=1}$. Figure 2A illustrates the oscillation among four values when $\alpha = 14$. The global relationship between α and multiple equilibria gives the remarkable pattern in Fig. 2B. Vertical dotted lines show the values α in (3) at which the number of stable points doubles. These are called "bifurcation" points for the parameter α. They follow a nearly geometric progression, so that the number of equilibria effectively becomes infinite and the Ricker curve produces "chaos" at values α somewhat higher than α_4. Still higher values α give additional regions of stability, bifurcation, and chaos.

When Bill proposed his recruitment model in 1954, it would have been impossible to foresee its complex consequences in Figure 2B. Computing technology has changed dramatically since then, and the link between algorithms and patterns has become a hot topic in modern science. While I prepared this talk, Wolfram (2002) published a lengthy book claiming that this link offers a whole new approach to the analysis of complex systems. The example in Fig. 1 above plays a role in his argument (op. cit., p. 411). Waldrop (1992) further documents the development of this approach in his account of the founding of the Santa Fe Institute. Bill's career spanned a period of great technological change, but he retained a genuine spirit of inquiry to the end. His interests in the structure of sunflowers (Fig. 1) and the chaotic properties of recruitment curves (Fig. 2) illustrate his lifelong fascination with creative ideas.

Acknowledgements

Bill had a great interest in Russian contributions to science, and perhaps he discovered the reference to Kuznetsov (1995) in that context. Similarly, Kuznetsov might have noticed the Ricker curve because of Bill's strong scientific reputation in Russia. Either way, Kuznetsov's book makes a remarkable contribution to the literature on nonlinear dynamical models. The author wrote it while in Amsterdam, but he cites work at the Research Computing Centre of the Russian Academy of Sciences, which was renamed in 1992 as the Institute of Mathematical Problems in Biology.

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NATURE, NURTURE, AND THE STOCK CONCEPT

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EXTENDED ABSTRACT ONLY: DO NOT CITE

> "The salmon of a given species may in a locality, e.g., a river, constitute a more or less distinct entity, for which the name "stock" is to be preferred. It is not known whether the differences between such local stocks are ever heritable."
>
> Pg. 106. Concluding summary of 1939 AAAS discussion on 'The migration and conservation of salmon" (Moulton, 1939)

While this conference is, to the best of my knowledge, the origin of "stock" in its fishery science usage, it was notable that debate still existed concerning the source of the acknowledged differences between the localized populations of salmonids. It is ironic that while Dr. W.E. Ricker was a contributing founder of the modern usage of the "stock concept" in salmon management, he preferred the original usage of biological race to describe these differences. In the original 1959 draft of his seminal paper on 'Heredity and environmental factors affecting certain salmonid populations' (Simon and Larkin, 1970), Dr. Ricker refers to stock as being non-committal to the importance of a heritable basis for these differences. Bill Ricker had already worked at, and left, the Pacific Biological Station by the time of this publication but he does not seem to have contributed directly to it. Over the next 20 years though, he amassed the background material to his 1970 publication that clearly provided the basis for hereditable and environmental bases to the differences between salmon populations that had fueled debates in the salmon literature since the beginning of that century.

> "In almost all cases where both genetic and environmental influences affecting natural stock differences among Pacific salmon and steelheads have been searched for adequately, both have been found; though sometimes one, sometimes the other, is relatively weak, or is infrequently expressed." (Ricker 1970)

Bill Ricker picked up the challenge and proved his beliefs through careful documentation of nature (genetic) and nurture (environment), and provided the population dynamic framework for management in the development of the Ricker stock-recruitment curve. Most people associated with salmon management over the past few decades were likely students of Bill Ricker's contributions, but in hindsight, I question that Bill would be particularly proud of our application, the state of salmon conservation, and the role of hatcheries in current salmon production.

Rather than focus on past impacts, this paper will consider the current re-assessment of salmon management practices along the west coast of North America. These assessments have been spurred by the loss of many populations and awareness of the risks associated with continued development and future climate change. Rather than being focused on what differences between populations have existed, the importance of understanding how salmon populations interact and how to maintain adaptability are being increasingly considered (which are issues that Dr. P. Larkin had emphasized since the 1970s).

Even if his 'students' have been unable to fully utilize what Dr. W.E. Ricker provide the basis for, the stock concept has been the fundamental management paradigm for over 50 years. Dr. Ricker and others provided the building blocks, the challenge now is to rebuild the stock concept into a more dynamic framework that recognizes the value of variation and inter-connectedness of localized spawning populations.

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THE ROLE OF PELAGIC OCEAN HABITATS

IN THE RELATIONSHIP BETWEEN

SPAWNING BIOMASS AND RECRUITMENT

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The relationship between the recruitment produced by the annual number of eggs produced by spawners, or a proxy thereof, is characterized by a family of functional forms. Oceanographic conditions influence the shape of these curves through shifts in production and shifts in carrying capacity. In this analysis we re-visit Ricker=s early considerations of the role of habitat and habitat quality in determining the shape of the functional relationship between spawners and recruits.

Ricker (1954) identified 8 types of population control mechanisms.

1. Prevention of breeding by some members of large populations because all breeding sites are occupied.

2. Limitation of good breeding areas, so that with denser populations more eggs and young are exposed to extremes of environmental conditions, or to predators.

3. Competition for living space among larvae or fry, so that some individuals must live in exposed situations.

4. Death from starvation or indirectly from debility due to insufficient food among the younger stages of large broods, because of severe competition for food.

5. Greater losses from predation among large broods because of slower growth caused by greater competition for food.

6. Cannibalism: destruction of eggs or young by older individuals of the same species.

7. Larger broods may be more affected by macroscopic parasites or microorganisms, because of more frequent opportunity for the parasites to find hosts and complete their life cycle

8. In limited aquatic environments there may be a >conditioning' of the medium by accumulation of waste materials that have a depressing effect upon reproduction, increasingly as population size increases.

In this study evidence for mechanisms 1 - 3 is examined using information on habitat quality and habitat availability from Shelikof Strait in the Gulf of Alaska.

Pelagic Ocean Habitats

We examine the potential influence of ocean forcing on Pelagic Ocean Habitats (POH) that expand and contract in three-dimensional space. The project utilizes water column profile data collected during Alaska Fisheries Science Center

(AFSC) acoustic trawl and ichthyoplankton surveys between 1993 and the present. Temperature - salinity profiles taken during selected cruises are used to characterize POH for walleye pollock (*Theragra chalcogramma*) stocks. These examples are used to evaluate the potential impact of climate shifts on POH, annual production and carrying capacity.

Walleye pollock is a semidemersal schooling fish that is widely distributed throughout the North Pacific in temperate and subarctic waters. In the Gulf of Alaska, major exploitable concentrations are found primarily in the Central and Western regulatory areas (147^{o}-170^{o} W Longitude). Pollock from this region are managed as a single stock that is separate from the Bering Sea and Aleutian Island pollock stocks. Major spawning concentrations of pollock in the Gulf of Alaska have been observed in Shelikof Strait and the Shumagin Islands.

Breeding habitats for walleye pollock are defined using AFSC have annual acoustic trawl surveys in the Shelikof Strait area. Water column profiles reveal a large estuarine-like system with a dilute upper layer, a strong halocline and gradually increasing salinity to the bottom. Time series of vertical profiles reveal interannual variations in the spatial distribution of water masses within the Strait. These differences are used to characterize potential shifts in the dimensions of spawning habitat.

Living space for fry (larvae and juveniles) is defined using information from NOAA= Fisheries Oceanography Coordinated Investigations (FOCI) program. The FOCI program has conducted ichthyoplankton surveys in the region of Shelikof Stait during the months of April and May since 1984. These surveys provide a second look at POH in the context of its impact on competition during the larval period.

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WILLIAM RICKER

AND THE HELLS GATE CONTROVERSY,

1938-1948

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Overview

William Ricker played an important role as a critic of the activities and scientific program of the International Pacific Salmon Fisheries Commission (IPSFC) in its first decade of scientific investigations, 1938-1948 (Evenden, 2000). This paper analyzes Ricker's participation in the IPSFC's surveys of the Fraser River sockeye in 1938, the research and restoration program conducted by the IPSFC at Hells Gate, and the content and context of the debate about the Hells Gate program sparked by a critical study published by Ricker (1947). Research is based on archival study in British Columbia, Washington State and at the National Archives, Ottawa. The approach is historical and contextual.

Studying Hells Gate

Hells Gate figures as a central, contested site in the history of Fraser River salmon. In 1912-14, railway construction in the Fraser Canyon triggered landslides at Hells Gate that obstructed salmon runs and led to short-term restoration efforts and increased regulation of the native fishery. In the following two decades, the commercial catch of Fraser River sockeye fell markedly and questions persisted about the Hells Gate site and its effects. Not until 1937 and the passage of the first Pacific Salmon Convention between

Canada and the United States, did sustained research on Hells Gate commence. The IPSFC, led by scientific director William Thompson of the University of Washington, conducted in-river fish tagging experiments were conducted to determine the migration times of different racial units. In the course of investigations at Hells Gate, scientists observed that many tagged fish did not pass the site. One of these scientists was William Ricker. In subsequent seasons, scientists sought to determine the success of sockeye in passing Hells Gate at different water levels. Various problems were encountered in executing this research and in collecting tag data from native fishers.

Restoration and Research

Following unusual blockage conditions at Hells Gate in 1941, widely publicized in the press, the IPSFC launched a restoration program to investigate means to reconstruct the Hells Gate site and ease salmon passage. Fluvial and engineering experiments were conducted in the United States, and IPSFC engineers designed a series of fishways to cut into the granodiorite walls of the Hells Gate site and provide conduits for salmon passage. In 1945, after the first set of fishways had been completed, the scientific data and analyses underpinning the restoration program were published for public scrutiny. William Thompson (1945) summarized and analyzed an enormous body of data collected in one of the largest research programs yet conducted in fisheries biology in British Columbia.

Critique and Controversy

William Ricker (1947) published a critique of Thompson's bulletin and called into question the experimental design at the foundation of the Hells Gate investigations. He suggested that too much emphasis had been placed on the role of Hells Gate to the absence of other relevant factors, most particularly fishing pressure. He asked if the IPSFC Hells Gate program was not, in part, related to the looming debate over fish and dams on the Fraser River. Ricker's critique produced an unpublished, polemical reply from Thompson, distributed to scientists, the press and politicians in Canada and the United States. Considerable debate emerged between Canadian and American scientists over the efficacy of the research conducted at Hells Gate, the reliability and productivity of Canadian fisheries science in the years prior to the establishment of the IPSFC, and of the wider ramifications of such disagreement for future scientific cooperation and funding.

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EXTENDED ABSTRACT ONLY - DO NOT CITE

EXTENSIONS OF THE

RICKER STOCK-RECRUITMENT MODEL

TO INCLUDE TIME-VARYING PARAMETERS

AND SPATIAL STRUCTURE

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EXTENDED ABSTRACT ONLY - DO NOT CITE

A good understanding of the Ricker stock-recruitment relationship is important for estimating productivity of Pacific salmon (*Oncorhynchus* spp.) stocks and managing them. However, the best-fit Ricker model for a given data set typically leaves large residual variation. Identification of environmental effects to account for some of that variation is hampered by short data series, measurement error, and natural variation in survival rates on short and long time scales.

We extended the Ricker stock-recruitment model in two ways. First, we used a multi-stock version of the model to incorporate environmental variables. Estimating model parameters across a large number of stocks simultaneously should improve the precision of parameter estimates and power to detect environmental effects. Second, in a separate analysis, we formulated the Ricker model in the context of a Kalman filter, which allowed the Ricker *a* parameter to

vary over time to reflect possible climate-driven changes. Such non-stationarity in productivity of salmon stocks has important management implications for harvest regulations and conservation.

Covariation Among Stocks and a Multi-stock Model

The basis of our multi-stock Ricker model was the observed positive covariation in spawner-to-recruit survival rates of pink (*O. gorbuscha*), chum (*O. keta*), and sockeye salmon (*O. nerka*) stocks. This covariation only occurred across local or regional spatial scales of several hundred kilometers (e.g. Peterman et al., 1998; Pyper et al., 2001; Pyper et al., 2002). Coastal sea-surface temperatures (SST) have similar spatial correlation scales, suggesting that covariation in survival rates among salmon stocks is driven by shared regional-scale processes in the coastal ocean (Mueter et al., 2002).

We therefore fit a multi-stock mixed-effects generalized Ricker model to stock-recruit data for all stocks of a given species and area, where "area" was either northern (i.e. Alaska) or southern (i.e. British Columbia and Washington):

$$(1) \qquad \log_e(R_i/S_i) = \alpha + a_i + \beta_i S_i + \gamma\, SST_i + g_i\, SST_i + \varepsilon_i$$

The α parameter is common to all stocks in an area and a_i is a stock-specific deviation from α. Similarly, γ is the common effect of SST on all stocks within an area and g_i is a stock-specific SST effect. We used spawner and recruit data over an average of 31 years for 120 stocks of pink (43 stocks), chum (40), and sockeye (37) salmon. SST_i were anomalies from long-term monthly means averaged across the coastal areas occupied by a given stock during the first four months of ocean life.

Warm anomalies in coastal temperatures were associated with *increased* survival rates of all salmon stocks from Alaska but with *decreased* survival rates of pink and sockeye salmon stocks from Washington and British Columbia (Mueter et al., 2002) (Fig. 1). Our results suggest that temperature effects are much more consistent across adjacent stocks than indicated by single-stock analyses, and provide precise estimates of mean SST effects within each area (Fig. 1). We therefore expect better estimates of the other parameters of model (1), which should improve the management advice based on the Ricker model.

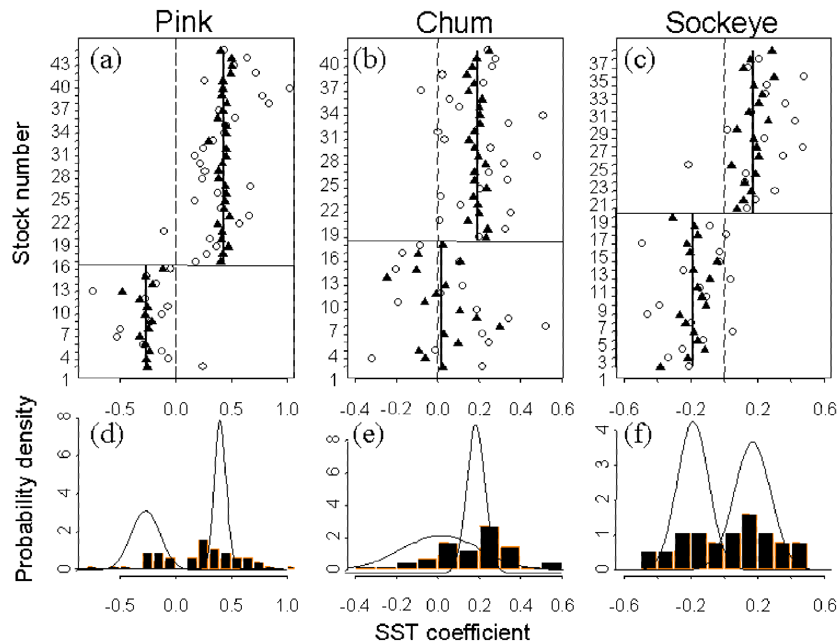

Figure 1. Estimated coefficients for effects of SST on $\log_e(R/S)$ for 120 stocks of pink, chum, and sockeye salmon. Estimates based on single-stock models (open circles in a-c) are compared with estimates based on mixed-effects models, which consist of a mean SST effect by area (γ in Eq. 1, vertical solid lines) and stock-specific random effects (g_i in Eq. 1; filled triangles show $\gamma + g_i$). Stocks in a-c are arranged along the Y-axis from south to north, with stocks from the northern and southern areas separated by a horizontal line. Bottom panels (d-f) show histograms of the fixed SST effects based on single-stock models and estimated probability density functions (smooth curves) for the estimated random SST effects based on multi-stock, mixed-effects models (Eq. 1). Reprinted by permission from Mueter et al. (2002).

Kalman Filter and Time-varying Parameters

There is growing evidence that productivity of many salmon stocks in the Northeast Pacific Ocean was higher in some decades than others due to altered climatic forcing. To meet conservation and other management goals, harvest regulations must respond in a timely manner to such non-stationarity in Ricker stock-recruitment parameters, but it is difficult to detect.

However, Peterman et al. (2000) demonstrated with Monte Carlo simulations that, if in nature the Ricker *a* parameter varies over time, estimating the Ricker stock-recruitment model formulated as a Kalman filter with a random walk system equation (equations 2 and 3) performs better at tracking those changes than the standard Ricker model approach in which parameters are assumed constant.

(2) $\log_e(R_t / S_t) = a_t - bS_t + v_t$, where v_t is ~N(0, σ_v^2)

(3) $a_t = a_{t-1} + w_t$, where w_t is ~N(0, σ_w^2)

Because of these simulation results, we applied a Kalman filter approach to reconstruct the historical sequence of Ricker a_t values for eight Bristol Bay, Alaska sockeye salmon stocks using smoothed Kalman filter estimates. We found strong evidence of non-stationarity in productivity (e.g., some stocks showed a tripling of the Ricker a_t parameter over 20 years, while others showed decreases), which has important management implications. In particular, in the presence of uncertain climate-driven changes in productivity of Pacific salmon, harvest rates and escapement goals might need to be revised appreciably and more rapidly than would be inferred by using a stationary Ricker model. For the Alaskan sockeye stocks, the Kalman filter produced estimates of optimal escapement that changed over time and differed considerably from both the optimal values estimated by a standard stationary Ricker model and from actual escapements. These results suggest that utilizing a Kalman filter approach that assumes time-varying parameters may improve on the standard Ricker model approach by producing greater benefits in periods of high productivity and lower risks when productivity is low.

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DYNAMICS OF FISH POPULATIONS DESCRIBED BY RICKER'S MODEL AND ITS REORGANIZATIONS UNDER THE WITHDRAWAL EFFECT

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The central task of fishery is the maximal sustainable yield, i.e. an optimum withdrawal from the population with preservation of the maximal reproduction for a long time. It is considered that fishery gain is proportional to amount of the trade efforts. If the value of trade efforts could be determined by order, the task of optimization of withdrawal would be considered to definition of an optimum share of withdrawal and optimum amount of efforts ensuring the most equilibrium level of withdrawal. Fixing optimal efforts we could “fishing” and synchronous transfer a population in an optimum sustainable level. The basic difficulty here is that the trade efforts fail to be fixed. Their changes in time are defined by some factors such as weather conditions, technical equipment, and fishery stock. Apparently, dependence of amount of the trade efforts on an exploited population plays here the large role.

For illustration of this situation let us follow a mathematical designation. The relation between the number (abundance) of the consecutive generation is described by recurrent equation

$$X_{n+1} = aX_n e^{-bX_n} - \frac{f_n aX_n e^{-bX_n}}{m + f_n},$$

and in relative number

$$x_{n+1} = ax_n e^{-x_n} - \frac{f_n ax_n e^{-x_n}}{m + f_n} \quad \text{by} \quad x_n = bX_n,$$

where x_n, x_{n+1} are the number of parents and recruits accordingly, a is a biotic potential, b is an ecological limitation, f_n is the fishery efforts in current year, m is the value of efforts ensuring half of maximum possible part of withdrawal. The first item is a reproduction (Ricker's curve) and the second item is the function of the withdrawal (annual catch).

For this model were obtained the tentative estimations of parameters on trade statistics data for real fish and crab populations. The values of annual catch and trade efforts were used as basic data designated accordingly as Y_n^* and f_n^*, and the model catches are equal

$$Y_n = \frac{kf_n ax_n e^{-x_n}}{m + f_n}, \text{ where } k=1/b.$$

The estimation of the model parameters consists in selection of such values of the parameters a, m, k and x_o, by which the sequence Y_n approximates a known sequence Y_n^* in the best way. The values of trade efforts are defined as $f_n = f_n^*$. This problem was decided by a usual method of least squares. As a result is shown what exactly the offered function of the craft allows in the best way to describe the catch dynamic of trade populations.

With estimated parameters it was evaluated the trade stock of four exploiting objects in each year of fishery. Also, by this data rows it was concretized the statistical dependence between trade efforts amount (f) and value of current stock ($F(x)$) or population size before the reproduction (x). It was shown that the efforts in most cases regular changed when population size increases and this change is approximate by power function $f = \gamma[F(x)]^\alpha$ or $f = \gamma X^\alpha$ sufficiently exact (the value of the determinant index is $0{,}62 < R^2 < 0{,}93$). The α parameter reflects the intensity of changes of efforts. As rule the effort amount increases with the degreasing of the population number. In this case the α parameter is negative. It is connected probably with such fact that fisher increases the trade efforts by small population size to ensure the required catch.

Conditions of the stability $\bar{x}_M$

$f = \gamma[F(x)]^{\alpha}$	$f = \gamma x^{\alpha}$
$-\dfrac{1}{1-\bar{x}_M} = \alpha_1 < \alpha < \alpha_2 = \dfrac{2-\bar{x}_M}{\bar{x}_M(1-\bar{x}_M)}$	$-1 = \alpha_1 < \alpha < \alpha_2 = \dfrac{2}{\bar{x}_M} - 1$
$m_0 = \left(\dfrac{\bar{x}_M}{1-\bar{x}_M}\right)^{\alpha-1}$	$m_0 = (1-\bar{x}_M)\bar{x}_M^{\alpha-1}$

The α parameter is an "indicator" of the fishery effect. If α appears less α_1 then the number passes to a new stationary level meaning, apparently, the degeneration of the population (zero equilibrium here is stable). If α appears more α_2 in the population there are **oscillations of number called by the craft from variable part of withdrawal.**

Now all models' parameters are known and it is possible the results of commercial fishing to analyze theoretically and the state of the corresponding commercial populations to assess. The model curves, as well as the bisector of the first coordinate angle are shown in Figure 1. As large is the area of the figure limited by the model curve and bisector of the first coordinate angle as the balance between maximal yield and maximal reproduction is more stable (population of herring). In case of walleye pollack this area is very low, therefore, there is an actual hazard of commercial overfishing. If the model curve comes nearer or lays under bisector, the population will inevitably vanish as an object of commercial fishing (halibut, Baltic herring).

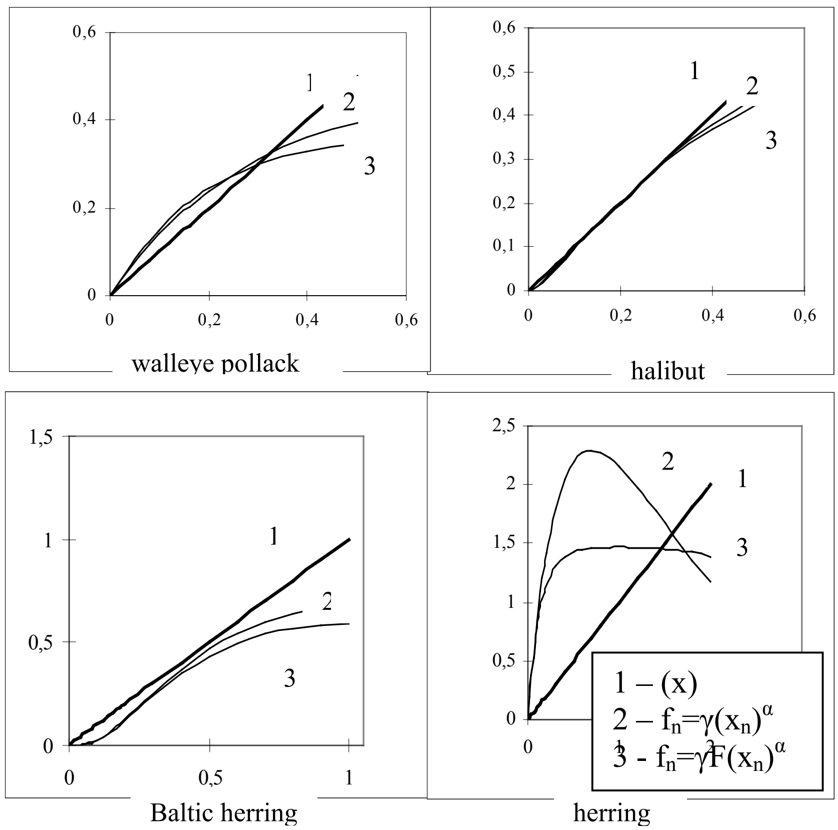

Figure 1. Simulation of the population dynamic

Thus, construction, analysis, and verification of a very simple mathematical model of population dynamics of commercial fish allows the following conclusion to be drawn: if fishing intensity is a nonlinear function of population size, fishing intensification inevitably causes either population size oscillations or population degeneration.