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RUMINATIONS ON THE DEVELOPMENT AND FUTURE OF POPULATION DYNAMICS MODELS IN FISHERIES

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ABSTRACT. I trace the development of fisheries models (i.e., fish population dynamics models of species subject to fisheries) to the 21st century. The first real efforts occurred in the period 1900–1920 with the work of Baranov (the "Grandfather" of fisheries population dynamics) and the formation of the International Council for the Exploration of the Sea (ICES). The establishment of the science occurred between 1920–1960 with multi-species modeling, age- and size-structure dynamics, and production models. Fundamental work during this time was done by Ricker (the "Father" of fisheries population dynamics), Beverton and Holt (the "Prophets" of fisheries population dynamics), Chapman, Dickie, DeLury, Graham, Gulland, Leslie, Lotka and Volterra, Russell, Schaefer, and Thompson. During this time, most of the work was deterministic and mathematical. Between 1960 and 1980, statistical methodology evolved greatly but was separate from mathematical advances for the most part. The development of statistical principles for the estimation of animal abundance was further enhanced by Arnason, Buckland, Burnham and Anderson and White, Cormack, Eberhardt, Jolly, Manly, Pollock, Ricker, Robson, and Seber, among others. Fisheries models evolved in a deterministic setting, with advances in age-structured models (Gulland, Pope, Doubleday), surplus production models (Pella, Tomlinson, Schnute, Fletcher, Hilborn), growth models, bioeconomic models (C. Clark) and management control models (Hilborn, Walters). The period 1980–2000 was the Golden Age. The integration between mathematics and statistics occurred when likelihood and least squares techniques were formally combined with mathematical models of population change. The number of fisheries modelers grew exponentially during this time, resulting in a concomitant increase in publications. A major advance in the 1990s has been the development of Bayesian and time series methods, which have allowed explicit specification of uncertainty. Currently, theory allows realistic modeling of age- and size-structured populations, migratory populations and harvesting strategies. These models routinely incorporate measurement error, process error (stochasticity) and time variation. But data needs often overwhelm the performance of models, and greater demands are being placed on models to answer complex questions. There has been poor communication between fisheries and ecological modelers, between fisheries researchers and statisticians, and among fisheries researchers in different geographic locales. Future models will need to deal better with habitat and spatial concerns, genetics, multispecies interactions, environmental factors, effects of harvesting on the ecosystem, model misspecification and socioeconomic concerns. Meta-analysis, retrospective analysis and operating models are some modern approaches for dealing with uncertainty and providing for sustainable fisheries. However, I fear that current attacks on single-species models and management may result in rejection of these advances and an attempt to substitute a less scientific approach.

KEY WORDS: History, fisheries model, fish population dynamics, population model, single-species model, fisheries management.

Introduction. Perhaps the most important development in the field of fisheries science has been the modeling of fish population dynamics associated with commercial, recreational and other fisheries (which I will call fisheries models, for short). These models provide the centerpiece of many fishery management systems: data and other inputs go into the models, and information about population status and management outputs comes out. These modeling efforts have further advanced our understanding of fundamental properties in the fields of mathematics, statistics and computer programming.

The purpose of this paper is to trace the development of fisheries models during the 20th century and to look to their future. As such, it reflects my subjective views of the important researchers and works in this field. This subjectivity probably includes my penchant for models that combine statistical and mathematical techniques in a rigorous way and my location in western North America; these two components tend to be correlated. Furthermore, I cannot claim to have done sufficient study to trace all the linkages between publication of results by particular authors and recognition of that work by other researchers. I have attempted to indicate the flow of ideas both in a geographical and chronological context, but admit that there is likely to be a lot of information about the flow of quantitative ideas about which I do not know.

I consulted the world literature on population models found in fisheries, ecology and human demography, including the books and articles by Beverton and Holt [1957], Keyfitz [1968], Ricker [1975], Seber [1982], Pauly and Morgan [1987], Gulland [1988a], Getz and Haight [1989], C. Clark [1985, 1990], Hilborn [1992], Hilborn and Walters [1992], Kruse et al. [1993], S. Smith et al. [1993], T. Smith [1994], Kingsland [1995], Funk et al. [1998], Quinn and Deriso [1999], Caswell [2000], Quinn [2002], Rozwadowski [2002] and reports by the National Research Council [1998–2000], as well as dug out many original papers in journals. The magnitude of available work is astounding and suggests that fisheries modeling has now reached the status of a mature science within the discipline of fisheries science.

I particularly single out the works by T. Smith [1994] (and an earlier book chapter, Smith [1988]) and Rozwadowski [2002]. Smith's book is really the only book that has been written about the history of fisheries science (but it stops in 1959). This work provided the mindset for my more limited aim of reviewing fisheries models and should be read by all students and researchers in the field of fisheries. Smith chastises our field for not paying more attention to history, and I dare say the comment applies more widely to other disciplines in the ocean and biological sciences. In my opinion, there is a tendency among modern researchers to ignore the historical literature, which results in failure to appreciate the origins of modern fisheries science and reinventions of already published methodology.

Rozwadowski's book focuses on the historical development of science within the ICES community. Given the importance of ICES in the development of both fisheries and marine science, this focused history gives much insight into the transition from maximizing fishery catch and/or efficiency to developing a conservative philosophy of fisheries management and sustainability. The book traces the development of key ideas related to understanding the changes in fish populations caused by physical, biological and/or human interactions, and shows the role played by scientists and organizations in this development. Further insights may be gained from a symposium proceedings on the history of ICES (Anderson [2002]).

It is curious that the study of population models in ecology and in fisheries have almost occurred in parallel universes. The book by Kingsland [1995] is an indispensable source for some of the early history of population ecology, which influenced the development of fisheries models. All the same, there is little cross-citation in these two literatures, despite similar developments in both. Some reasons for this separation include: (1) Researchers in fisheries and in ecology are in different departments or agencies, usually publish in different journals and go to different meetings. (2) Much ecological study is terrestrial, whereas much fisheries study is marine. (3) Data collection systems in fisheries and ecology are different, because the fishery is a major source of removals from the population and hence a major source of information. (4) The economic and social values of fisheries have meant that sources of funding are more plentiful and diverse. (5) Because the magnitude and types of data collected from fisheries systems can be enormous compared to that from terrestrial systems, different model structures are necessary.

Similarly, statistical advances in fisheries science are almost exclusively found in the fisheries literature. Few statisticians have been involved in fisheries modeling, and a whole class of methods, based on likelihood and Bayesian techniques, are unlike anything found in the mainstream statistics literature. Part of the problem has been that much of statistical theory involves the world of linear models, but nonlinearity of most population processes has required the development of alternative statistical approaches to solve fisheries problems. Another reason is that much funding for statistical research comes from other fields such as medicine, education and business, so that there is strong competition for the attention of statistical researchers, directed towards other problems.

The thesis I establish in this paper comes from my review of the literature and from my experiences in providing scientific advice to fishery management agencies and personnel. In my view, the 20th century saw the strong monotonic development of fisheries models for fish population dynamics, which culminated in a Golden Age between 1980 and 2000 (Figure 1). The Golden Age is now over. Current models and management tend to focus on a single species and are under attack because they purportedly: (1) don't incorporate species interactions, (2) don't sufficiently consider precaution, (3) don't operate on temporal and spatial scales of interest and (4) don't consider the ecosystem (NRC [1998a], [1999]). While these criticisms have some validity, they are often overstated because the model omissions can

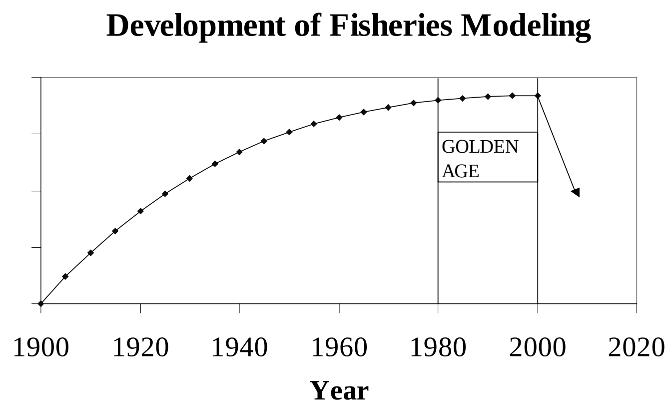

FIGURE 1. My view of the development of fisheries population dynamics models. A steady progression occurred in the 1900s, leading to a Golden Age between 1980 and 2000. I predict that there will be a decrease in new efforts in this discipline in the 21st century.

often be addressed (Quinn and Collie [in press]). Nevertheless, we may be seeing a paradigm shift that: (a) moves away from science-based management by de-emphasizing modeling and knowledge, (b) promotes "feel good" conservation strategies, (c) results in drastic economic and social consequences to the harvesters, but (d) attempts to reconcile new and competing objectives for fisheries and resource management.

Before 1900. My exposition is broken into different time periods which should be understood to be approximate. As explained by Smith [1994] little attention was devoted to the understanding of fish populations before the 20th century. The natural historian and physiologist Thomas Huxley conveyed the typical point of view in 1884 when he wrote that fish resources are essentially inexhaustible and man's ability to harvest is limited. This view changed rapidly toward the end of the 19th century as one fishery after another around the world resulted in reduced fishing success and likely depletion of the fish resource. Huxley himself helped form the Fishery Board of Scotland to prevent overfishing and secured funds and regulatory authority. Concerns about overfishing led to the creation of the International Council for the Exploration of the Sea in 1902; one of its first standing committees concerned overfishing (Rozwadowski [2002]).

Nevertheless, there were population dynamics studies done before 1900 with the focus on humans. The exponential growth law was explored by John Graunt, 1662; Linnaeus, 1742; Benjamin Franklin, 1751-1760; Thomas Malthus, 1798; and Charles Darwin, 1859 (Caswell [2000]). Verhulst derived the logistic growth model in 1838, though earlier Malthus recognized density dependence and food limitation (Quinn and Deriso [1999]). In his view, food increases arithmetically while populations grow geometrically, leading to fundamental limitations in populations. Gompertz developed his growth model in 1825. These early models became the basis for more complicated models in the 20th century, although many times they had to be rediscovered. Life tables (tables of mortality and fecundity by age) were compiled by the Romans in the 3rd century AD; Graunt, 1662; Halley (the famous astronomer), 1693; and Euler, 1760 (Caswell [2000]). The analysis of age structure is one of the most important aspects of fisheries models and owes much to life table analysis. Ecologists and fisheries scientists routinely conducted life table analysis in the 20th century. For example, Johan Hjort gained insights by studying life tables of Norwegian fishermen (see Smith [1994, pp. 124-128]).

1900–1920 First Efforts.

F.I. Baranov. I think of Fedor (Theodor) Ilyich Baranov (Baranoff, pronounced Bah-rawn'-off) as the Grandfather of fisheries population dynamics. Born in 1886, he "loved nature and was captivated by fishing" (Andreev in Baranov [1976]). He was Professor at the Moscow Agricultural Academy (1915–1930) and then head of the Dept. of Commercial Fisheries in Mosrybvtus (1930–1959). He wrote three of the first articles on fisheries models: "The theory of overfishing" [1914], "On the question of the biological basis of fisheries," written in 1916 and published in 1918 and "On the question of the dynamics of the fishing industry" [1925]. He also wrote a book called *Commercial Fishing Technique*, also known as *Theory and Calculation of Fishing Gear*, which appeared in four editions with the last edition in 1960. This book dealt mainly with the mathematics of fishing gear rather than fish populations.

Andreev concisely summarizes Baranov's contribution in the introduction to Baranov's collected works [1976–77]:

> Baranov established a functional correlation between the size of the fish stocks in a water body and the magnitude of the catches in it, and on the basis of this correlation concluded that the catch is the basic and decisive factor determining the state of the raw material reserves. According to his theory, without taking fishing into account one cannot correctly regulate fishing, assess stocks and correctly forecast their state. Baranov believed that the reduction in the numbers of fish due to fishing leads to a quantitative and qualitative change in the fish population.

Thus, Baranov recognized the exhaustibility of fish resources and man's ability to overfish.

Apparently, Baranov's colleagues thoroughly criticized his mathematical work, some of which is included in the 1976–77 collection. He himself seemed to have a heroic view of his task as a progenitor of a new field:

> Better an incomplete theory than no theory at all. A published theory becomes immediately subject to the scrutiny of a thousand eyes and heads. If the erroneousness of a theory is not detected immediately, it does not stand up to the great criterion of practice and cannot survive long. Lack of any theory at all makes it possible to stray forever.

As shown in his letters and addresses, he attempted to address criticisms of his modeling throughout his career (Baranov [1977]). I think that he was bewildered by the intensity of criticism, but he also seemed to keep a sense of humor, as shown from the following excerpt from a speech given in 1951 to the All-Union Conference on Fishery Problems:

> For 25 years now ichthyologists have been criticizing my old works... [F]ive objections were raised. First objection: the theory is irrelevant because it speaks of the effect of fishing on the abundance of fish and the fish population, and such an effect does not exist. Second objection: the theory is one-sided because it ignores natural factors. Third objection: the theory is based on incorrect methodological foundations since it proceeds from abstract notions. Fourth objection: the theory is methodologically incorrect because it uses a mathematical method. Fifth objection: the theory is incorrect because it leads to conclusions which are unacceptable to the

critics. I shall try and clarify the methodological errors which, in my opinion, are connected with these objections.

His most seminal contribution, from the 1918 paper, is the derivation of the theory of mortality for a year-class and its separation into natural and fishing mortality. This derivation starts with the differential equation for mortality and its solution (Figure 2a), from page 5 of the translation. Written in modern terminology, the solution for abundance is $N(t) = N_0 \exp(-Zt)$, in which N_0 is initial abundance of the year-class and Z (his k_1) is its instantaneous total mortality. Some nine pages later on page 14 of the translation, the separation into components occurs, as presented by the fractions of mortality ascribed to natural causes and to fishing (Figure 2b). Expressed in terms of annual catch (C) as a function of abundance (N), fishing mortality (F, his k_2) and natural mortality (M, his k_0), the resultant equation

$$C = N_0 \frac{F}{Z}(1 - e^{-Z}), \quad \text{with } Z = F + M,$$

became known as the Baranov catch equation (e.g., Ricker [1975]). This equation is probably the most used in all of fisheries modeling.

Baranov undertook length- and age-based analyses, per-recruit analyses, examination of catch curves and nonequilibrium analyses of yield in his papers which anticipate modern approaches. He did have to make the simplifying assumption that length and age are linearly related, which we now know is too simplistic. All the same, his work was eventually recognized and appreciated by Ricker, Beverton and Holt, Thompson, Russell, Graham, Silliman, F.N. Clark, and C. Clark, among others, as early as the late 1930s (per Andreev and Rozwadowski). His 1918 and 1925 papers were translated three different times (by Ricker in 1945, by Schaefer [date unknown], and in the 1976–77 collected works). In particular, Ricker viewed Baranov as a mentor even though he never met him. It is incredible to think that Baranov did his work almost 30 years ahead of most other work in fisheries modeling.

International Council for the Exploration of the Sea (ICES). ICES was established in 1902 (Smith [1988], [1994], Rozwadowski [2002]) under the leadership of Swedish oceanographer Otto Pettersson and many other scientists at a time when there was a strong spirit of internationalism. Two instrumental scientists were C.G. Johannes

Petersen (who developed the first mark-recapture estimator and a disk tag) and Friedrich Heincke (who estimated mortality from a catch curve). The issue of overfishing was debated early on, suggesting that the theory of inexhaustibility was rapidly being debunked by the start of the 20th century. For essentially the first time, the systematic and scientific inquiry into the dynamics of fish populations commenced. ICES established data collection systems and scientific studies about recruitment, stock identity, movement, abundance and aging. ICES scientists from the onset of the Council have been motivated by the desire to develop a theory of fishery science that could be used for the rational and conservative management of fish stocks (Rozwadowski [2002]).

Johan Hjort brought a focus on recruitment to fish populations during early life history (his critical period hypothesis of 1914, for example). The recognition of recruitment variability as being a prime factor in determining the size of fish populations was quite savvy and has resulted in advances in fisheries modeling through stochastic elements and incorporation of environmental data into population models. Smith [1994] described the insights gained by ICES scientists from the First Great Fishing Experiment (better known as World War I); Baranov also recognized the War as an experimental situation for fish stocks and used the concept as the basis of his 1925 paper. After fishing ceased during the war years, fish stocks were much more abundant after the war. This event demonstrated how important fishing could be in depleting fish populations, although some people thought it was related to environmental conditions. (This theme of fishing versus the environment persists to this day.) But the same thing happened in World War II, suggesting that overfishing was the proximal cause. Therefore, methodology was needed to determine how many fish could be taken from a fish population, which required study into the dynamics.

1920-1960 Establishment of Science. Various mathematical models emerged during this period for expressing the changes in a population, falling into two main categories. The first category is simple, pooled-stock dynamics, in which there is no explicit accounting of age or size structure. The second category is age- and size-structure

Thus, denoting by the letter n the abundance of any group of fish (of one age), and time by the letter t, we come to the conclusion that the decrease dn in the number of fish of this group is a small space of time dt is proportional to the abundance of that group and therefore

$$\frac{dn}{dt} = -k_1 n,$$

where k_1 is a coefficient, the same for all groups. Let us integrate this expression. We get

$$\frac{dn}{n} = -k_1\, dt, \text{ or}$$

1) . . . . $\log n = -k_1 t + \log C$, or

2) . . . . $n = Ce^{-k_1 t}$

Where C is a derivative constant, introduced in the integration.

(a)

$$\text{annual decrease from natural death} = \frac{\varphi\, k_0}{k_2 + k_0}$$

$$\text{annual decrease from fishing} = \frac{\varphi\, k_2}{k_2 + k_0}$$

(b)

FIGURE 2. (a) Baranov's [1918] derivation of the exponential decay equation for a year-class (p. 5); (b) The Baranov catch equation (p. 14), expressed as the annual decrease from fishing: k_2 = instantaneous fishing mortality, k_0 = instantaneous natural mortality, φ = annual death fraction = $1 - \exp[-(k_2 + k_0)]$, $k_2 + k_0 = k_1$ [instantaneous total mortality in (a)] (from Ricker's translation).

dynamics built on individual year-classes. The first type emphasizes changes over time in the total population; the second emphasizes the fate of individual year-classes.

Pearl, Lotka, Volterra et al. Within the first type, Raymond Pearl (with L.J. Reed) in 1920 rediscovered and popularized the logistic model of Verhulst from 1838. The logistic model is the centerpiece of much of fisheries modeling, leading to the theory of maximum sustainable yield (discussed below).

Lotka (who was hired by Pearl) and Volterra independently developed extensions of the logistic for multiple species in the 1910s and 1920s. Volterra's work was directly motivated by a fisheries problem posed by a relative. Apparently Volterra's papers received wider attention than Lotka's, which led Lotka to write papers claiming precedence (Kingsland [1995]).

Lotka's 1925 work, *Elements of Physical Biology,* was an attempt to develop a general theory based on mathematics: "The ideal definition is, undoubtedly, the quantitative definition, one that tells us how to measure the thing defined" (p. 19). His interest in population models was long-standing, dating back to the 1907 paper, "Relation between Birth and Death Rates," in *Science.* He posited a fundamental system of differential equations of the form

$$\frac{dX_i}{dt} = F_i(\{X_i\} \mid \mathbf{P}, \mathbf{Q}),$$

in which a collection of species $\{X_i\}$ is affected by environmental and biological parameter sets $\mathbf{P}$ and $\mathbf{Q}$ through the functions $\{F_i\}$. Motivated by chemical kinetics, he used Taylor series expansions and phase plane analysis to explore the behavior of this system, as well as delved into metaphysical issues. While he recognized the limitations of the abstractions of mathematics, he also believed: "such abstractions are a necessary ... and a very effective aid to our limited mental powers, which are incompetent to deal directly with unexpurgated nature in all its complexity" (p. 301). His collected works number close to 100 publications across a variety of fields.

Gause, Kostitzin, Bodenheimer, Deevey, Allee, and Andrewartha and Birch also contributed papers related to population regulation, density-dependence and the role of the environment (Caswell [2000], Smith [1994], Kingsland [1995]). Kingsland gives a thorough perspective of the zeitgeist of Pearl, Lotka, Volterra and their colleagues in ecology, showing the lines of scientific inquiry and development of methodology.

Within the second type, life tables and age distributions were formulated during this period. In particular, Lotka developed in his 1925 book the essential theory of deterministic age-structured populations in addition to multispecies models. The resulting life table analysis was the standard technique for analyzing age-structure, appearing in most ecology textbooks, until matrix methods became more favored in the latter part of the 20th century (Caswell [2000]).

W.F. Thompson. W.F. Thompson (1888–1965) was a fisheries research giant during this period. He attended University of Washington (UW) and Stanford (B.S. 1911, Ph.D. 1930). He studied Pacific halibut in British Columbia from 1914–1917 and worked at California Fish and Game from 1917–1924. He was Executive Director of the newly-founded International Fisheries Commission (later International Pacific Halibut Commission) from 1923–1940 which was housed at UW. He started aging studies of Pacific halibut, began a program of collecting logbooks from harvesters and a program to mark halibut for movement and growth, developed yield theory (Thompson and Bell [1934]) and was responsible for stringent management measures thought to rebuild the fishery in the 1930s. He was also Professor at UW from 1930–1958. In addition he was Research Director of International Pacific Salmon Fisheries Commission (which was housed at UW starting in 1937). He became the first director of the UW Fisheries Research Institute during 1947–1958. Notable among his publications was the Thompson-Burkenroad debate in the 1940s and 1950s, in which Thompson contended that fishing regulation was responsible for the increase in the Pacific halibut population in the 1930s (Skud [1975]). Burkenroad argued it was due to beneficial changes in the environment. Both sides used data and analysis to support their arguments, but in retrospect, both fishing and the environment were important. Many scientists including Graham, Beverton and Holt, Dickie, and Ricker joined the debate, considered one of the most intense in the fisheries literature (Skud [1975]).

ICES. ICES played a major role in establishing the scientific basis for fisheries models. E.S. Russell, director of the Lowestoft Laboratory in Great Britain, provided a heuristic context in 1931 for the development of fisheries models by writing the simple relationship

$$\begin{aligned} N_{t+1} = N_t &+ \text{Recruitment} + \text{Growth} - \text{Natural Mortality} \\ &- \text{Catch} \quad \text{(Smith [1994])}. \end{aligned}$$

Other researchers used this formalism to fill in the details of population processes.

Another way in which ICES played a critical role was in education. ICES sponsored seminal workshops on a variety of topics (Rozwadowski [2002]). Generally the audience for these workshops was mostly European, because Canada and the United States did not become members until 1967 and 1973, respectively. The volume developed by Beverton and Holt (see below) became known as the "Bible" both in European circles and throughout the world. Finally, the wide range of committees and working groups provided opportunities for learning, collaboration and cooperation that defined the success of ICES as an institution and as a model for fishery management agencies around the world.

Hjort and his colleagues posited in 1933 that a fishery would have an optimum yield derived from the equilibrium conditions of a population model. Later known as maximum sustainable yield (MSY), it was found from the logistic model at the inflection point corresponding to when the population is most productive. MSY is still the main benchmark for the exploitation of fish populations. The typical parabolic equilibrium relationship between yield (or productivity) and biomass is shown in Figure 3, showing the MSY point.

Michael Graham was a professor who became Director of the Lowestoft Laboratory and was a key player in ICES and fisheries science around the world. In 1935 he developed further the theory of optimum yield based on the logistic model. Equally impressive was his foresight in employing bright, young scientists (Hulme, Beverton and Holt) to quantify fisheries methods, which led to a two-page article by them in *Nature* in 1947.

German marine biologist Adolf Buckman succeeded Heincke in 1923 and worked on differential equation models for the relationship between fishery yield, fishing intensity and growth rate (Rozwadowski [2002, p. 91]). Due to his work being in German, a bad feeling about Germans because of the war and a rivalry with Michael Graham, his work has apparently been lost to us.

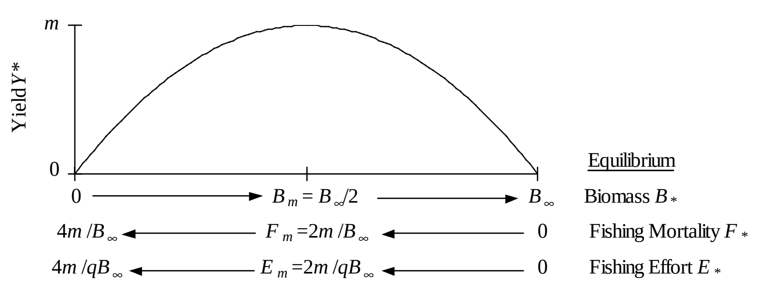

FIGURE 3. Equilibrium yield as a function of biomass, fishing mortality and fishing effort. The MSY point (m) is in the middle (after Quinn and Deriso [1999, Figure 2.3]). B_∞ is carrying capacity and q is catchability.

Beverton and Holt. Ray Beverton (1922–1995) and Sidney Holt continued to work on quantitative fisheries models which led to the most important work in fisheries models at the time in 1957.

> We make no apology for the fact that much of what is to follow is mathematical in nature. It is now generally accepted by fishery naturalists, and in fact by most workers dealing with population problems, that mathematics is an indispensable tool in their studies.

Their near-decade of work (1947–1953) resulted in the development of a comprehensive theory of fishing that integrated growth, mortality and recruitment, as anticipated by Russell's equation. The book dealt with regulation (minimum size, fishing mortality, refugia, optimum yield, economic considerations), provided rudimentary methods of parameter estimation, investigated growth and feeding, and examined spatial variation and movement. They were inspired by von Bertalanffy's views on open system theory and work on human growth models [1938]. Most of the work was mainly deterministic but stochasticity was recognized as being important. Their work remains the standard for year-class (dynamic pool) models.

Beverton and Holt were aware of Baranov's methods, even publishing a correction of one of Baranov's analyses in their volume. I view their contribution as a direct elaboration and extension of Baranov's year-class approach. They were intimately familiar with the extant literature of population models and cited Ricker's work in their volume. The major difference between Beverton and Holt's work and Ricker's work is that the former is more mathematical and the latter is more statistical in flavor. A special issue was published in 1998 to commemorate and evaluate the influence of the 1957 volume on fisheries research (Pitcher and Pauly [1998]). Holt [1998] acknowledged the legacy of Baranov and Russell, but also noted that their work did not have a major influence on the 1957 volume (Holt, pers. comm.). Beverton [1998] (published from notes after his death) did not mention Baranov at all, although he did acknowledge Ricker's work. Interestingly, Beverton [1998] viewed the work on self-generating population models in the 1957 volume more important than the work on per recruit models, although most researchers are unfamiliar with the former. In light of the biblical designation of their volume by several researchers, I think of them as the Prophets of fisheries population dynamics!

Finally, substituting for R' from (4.2) and integrating gives*

$$Y_W = FRW_\infty e^{-M\rho} \sum_{n=0}^{3} \frac{\Omega_n e^{-nK(t_{\rho'} - t_0)}}{F + M + nK} \left(1 - e^{-(F+M+nK)\lambda}\right) \quad .. \qquad (4.4)$$

where

$$\lambda = t_\lambda - t_{\rho'} = \text{the fishable life-span}$$

FIGURE 4. The yield of a year-class, expressed as a function of biological parameters and management parameters (see text) from Beverton and Holt [1957, p. 36] with kind permission of Kluwer Academic Publishers.

I show in Figure 4 one key equation from their book (p. 36). This equation shows the synthesis of population and management processes in explaining the yield from a fishery. It is related to fundamental biological parameters: the recruitment R of a year-class at a reference age t_ρ, natural mortality M, von Bertalanffy growth parameters W_∞, K, t_0, and the oldest age t_λ, under the assumption that weight is an isometric (cubic) function of length. Management parameters are the knife-edged age of entry $t_{\rho'}$ into the fishery (with $\rho = t_{\rho'} - t_\rho$) and the fishing mortality F. Consequently, one can learn about ways to maximize yield per recruit as a function of management parameters by plotting yield isopleths, as shown in their Figure 17.14.

After their work was completed, Holt moved to the Nature Conservancy and then the U.N. Food and Agricultural Organization (FAO) and turned his interests to whale conservation, participating in several meetings of the International Whaling Commission. Beverton remained active in fisheries for awhile, pursuing relationships between life history parameters (such as the positive correlation between M and K). After a long period as an administrator he returned to the fisheries field as editor of the *ICES Journal of Marine Science*. He embarked on a lecture tour of the U.S. in conjunction with the re-release in 1993 of the 1957 volume. He was a gentleman and a scholar, both kind and thoughtful.

William E. Ricker. I believe that nobody has made more contributions to the development of fisheries models than William E. Ricker (1908–2001). I think of him as the "Father" of population dynamics because of the breadth of his contributions, the length of time he was active in the population dynamics field and his recognition of the importance of statistics in modeling. He was at Indiana University in the 1940s and at Canada's Pacific Biological Station in Nanaimo, B.C. thereafter. Ricker had the rare ability to blend statistical wisdom with mathematical elegance within a grounding of biological principles. Two important early works illustrating this ability are "Relation of CPUE to Abundance and Rate of Exploitation" [1940] in just the fifth volume of the *Journal of the Fisheries Research Board of Canada (JFRBC)* (the predecessor to *Canadian Journal of Fisheries and Aquatic Sciences (CJFAS)*) and "Some Applications of Statistical Methods to Fishery Problems" [1945] in the *first* volume of *Biometrics*.

His classic work "Stock and Recruitment" [1954] in volume 11 of *JFRBC* is matched only by Cushing's insightful studies (Cushing [1971]). The 65-page paper deals with theory of population regulation, compensatory mortality and control mechanisms. The so-called Ricker spawner (S)-recruit (R) curve [$R = \alpha S \exp(-\beta S)$] is derived from a simple model of predation. It is clear that Ricker understood the concept of replacement related to reproductive potential for both semelparous and iteroparous populations; the formal mathematics for the latter case did not appear for almost 40 years (Getz and Haight [1992]). He provided examples ranging from water-fleas to salmon. He discussed the effect of fishing on reproductive potential and proposed a general theory of recruitment in relation to predation. Figure 5 shows the Ricker equation as published (in nondimensional units for generality) and the family of curves it produces. In 1971, he followed up on this work by publishing "Critical Statistics from Two Reproduction Curves" (the Ricker and the Beverton-Holt curves). He published widely on population dynamics and cycles in Pacific salmon and on maximum sustainable yield in the presence of natural fluctuations and mixed stocks.

Ricker helped to educate at least two generations of fishery scientists about fisheries models by publishing handbooks in 1948, 1958, 1971 and 1975. The 1948 volume contained mainly the basic theory of mortality, catch curve analysis and mark-recapture methodology. The 1958 volume had greatly expanded coverage of population models (linked to Baranov), surplus production (linked to Schaefer), per recruit models (linked to Beverton and Holt) and a variety of other methodology from literature from around the world (including Russia and Norway). The 1975 volume was structurally similar to the 1958 volume with updated

Substituting $1/e$ for s_1 in (7), we thus finally obtain the expression

$$we^{1-w}. \tag{10}$$

This shows the actual level of reproduction as a fraction of the maximum, when w represents the ratio of the actual density of mature stock to the density which gives maximum reproduction. Values of (10) are plotted as curve B of Figure 33.

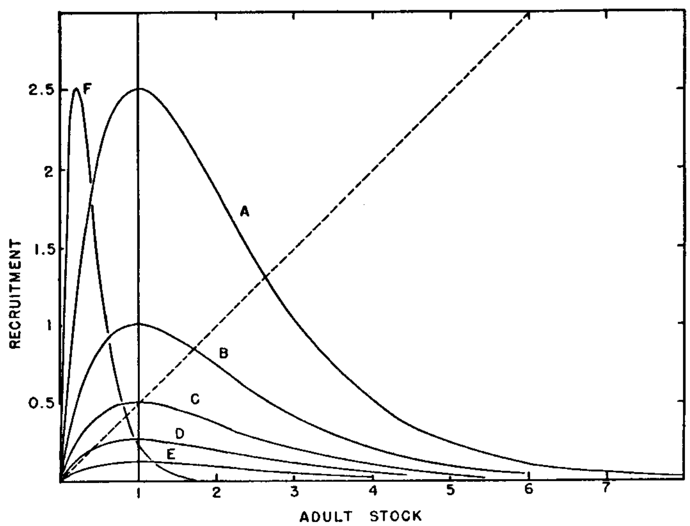

FIGURE 33. Graphs of we^{1-w} ("recruitment") plotted against w ("adult stock"). Curve B corresponds to the axes as labelled; the other curves are obtained by varying the ordinate and (for F) abscissal scales.

FIGURE 5. First appearance of the Ricker spawner-recruit curve from Ricker [1954, pp. 611–612].

coverage of new methods. The 1971 volume was an edited volume written for freshwater fisheries and aquatic scientists. The writing style was lucid, intuitive and structured to allow researchers to learn new approaches. His "spreadsheet" approach in his handbooks (e.g., Ricker [1975, p. 320]) provided easy algorithms for carrying out sophisticated computations of spawner-recruit relationships, equilibrium yield and yield-per-recruit, for example. This made it possible for biologists with minimal mathematical and statistical training to apply valid methods to fisheries problems.

Among his many other important works, Ricker contributed to the field of statistics. In 1973 he published "Linear Regressions in Fishery

Research" which led to an extensive debate in the fisheries literature with statistics professor Jolicoeur. Ricker was interested in the problem of errors in both variables in a linear regression, a common situation in fisheries. He developed the AM and GM approaches for this problem and showed how to use them in his 1975 handbook. While this work has been supplanted for the most part by more modern methods, it shows that he was able to operate at the interface of statistics and fisheries science.

Brief summations of his life are found at `www.phys.ocean.dal.ca/ccffr/ricker.html` and `http://www.pac.dfo-mpo.gc.ca/sci/pbs/english/RICKER_e.htm`, and a comprehensive obituary was published in *CJFAS* by Beamish et al. [2003]. He published 296 papers and books, 238 translations and 148 other manuscripts. He was editor of *CJFAS* for 12 years starting in 1950 and "turned what was a parochial journal into perhaps the world's most influential fisheries science publication" (Beamish et al. [2003]). In addition to being one of the foremost scientists of his time, he was also interested in birds, plants, insects (a world authority in the taxonomy of stoneflies), geology, classical music, Canadian history, languages and archeology. He wrote fiction and poetry and played music and sang. He was known for his generosity, modesty and tranquility. Among other honors, he was made an Officer of the Order of Canada and had a research vessel named after him (both in 1986).

Sette and Schaefer. A strong research laboratory developed in California in the 1940s, partly under the direction of Oscar Sette (Smith [1994]). Sette developed a comprehensive research program on sardines at the California Bureau of Fisheries. Papers by Silliman and F.N. Clark about sardine population dynamics are cited in Ricker's 1975 handbook. Milner Schaefer (1912–1970) used Sette's data to develop a nonequilibrium surplus production model for the sardine fishery in 1951. Schaefer [1954] refined this method and applied it to sardine, halibut and tuna. The beauty of his approach is that it derived annual surplus production (ASP) from empirical observations and used those values of ASP to derive equilibrium parameters such as MSY from the logistic model of Pearl, Hjort, and Graham. Gerald J. Paulik (Professor, University of Washington) stated in 1968: "In spite of the growing sophistication of theoretical biology and, in particular, mathematical modeling in fisheries, Schaefer's equilibrium yield model is probably the single most important conceptual tool available to anyone concerned with the dynamics of an exploited natural population." (`http://www.oac.cdlib.org/dynaweb/ead/ucsd/scripps/schaefer`).

Gordon [1954] combined the Schaefer model with economics theory to show that common property resources lead to dissipation of economic rents from a fishery. This paper inspired several bioeconomic papers in subsequent years (see below).

Estimation of Animal Abundance: Chapman, DeLury, Fry, Dickie. A formal basis for the estimation of animal abundance originated in the 1940s and 1950s. A key person in this development was Professor Douglas Chapman (1920–1996). Originally in the mathematics department at University of Washington, he became interested in fisheries problems as early as 1948 and taught his first class to fisheries students in 1949. He developed statistical theory of mark-recapture and catch-effort methods in the 1950s and 1960s. His 1951 paper established the hypergeometric distribution as the basis for the single-release, single-recapture mark-recapture experiment, leading to a bias-corrected estimator of abundance in use to this day. He became a guiding light for the application of statistical methods in fisheries research. He worked with IPHC to develop yield theory for Pacific halibut (Chapman et al. [1962]), and was instrumental in bringing science to the management of whales (International Whaling Commission (IWC), with K. Radway Allen, Sidney Holt and John Gulland (e.g., Chapman [1974])). He also developed strong programs in quantitative science at UW and became Dean of the School of Fisheries.

At the same time, Canadian researchers were also promoting the modeling of populations and statistical methods for the estimation of animal abundance. D.B. DeLury of the Ontario Research Foundation made several contributions, but his best known [1947] is the development of depletion estimators for estimating abundance. He showed that functions of catch per unit effort were linearly related to either cumulative catch or effort, elegantly combining basic population dynamics with statistical theory. In 1949, F.E.J. Fry of the University of Toronto developed the concept of a virtual population, the minimum abundance of a year-class that must have been present at any age (from the cumulative catches of a year-class). Virtual population analysis (VPA) proved to be the progenitor of age-structured stock assessment models developed in the 1960s by ICES and others (see below). L.M. Dickie of Dalhousie University and Bedford Institute of Oceanography also contributed important papers around this time (e.g., Paloheimo and Dickie [1964]).

Leslie Matrix. The final contribution from this period that I will mention is one of the most important. P.H. Leslie in 1945 developed the theory for age-structured populations based on matrix methods (Caswell [2000], Quinn and Deriso [1999]). The Leslie matrix contains fecundities and early life survival in the first row and survivals at other ages on the off-diagonal. This discrete formulation made the understanding of age-structured dynamics much easier than with the continuous life table analysis. Ignored for almost 20 years (as explained by Caswell [2000]), the Leslie matrix formulation and its extensions are now the standard for age-, length- and spatial-structured models in fisheries. The basic Leslie matrix model with constant parameters exhibits the same long-term behavior as the exponential model for the most part, but nonlinear and stochastic extensions connect with the Russell equation, surplus production models and the dynamic pool models of Beverton and Holt (Xiao [2000]). Leslie also made several contributions to mark-recapture and other methods for estimating abundance, and in particular, developed a depletion model related to cumulative catch before DeLury (Leslie and Davis [1939]). Chapman, Ricker, and others developed extensions to the depletion models of DeLury and Leslie (see Seber [1982]).

Distrust of Modeling. All throughout this period of time, there was much resistance among biologists to the developments of mathematical and statistical models (as noted in DeLury's paper, for example). At the National Science Foundation of the United States, there was widespread distrust of models for natural populations well into the 1970s (Keith Benson, pers. comm.). Many biologists and other scientists felt that the assumptions underlying the methods were too unrealistic. Part of the problem is that biologists (and harvesters, too) are often focused on detailed observations that are in conflict with the generalities and simplifications of mathematical models. At the same time, mathematicians and statisticians are looking for general patterns and sometimes avoid dealing with small-scale variation.

At the same time, the ICES community was very enthusiastic about modeling, likely due to the vision and influence of Graham and others (Rozwadowski [2002, p. 163]): "In 1957, ICES, FAO, and ICNAF (International Commission for Northwest Atlantic Fisheries) came to general agreement on the importance of population dynamics for the future of fisheries science." Because a major responsibility of ICES evolved to be the provision of scientific advice to various commissions, modeling was viewed as the only means to the development of rigorous and objective advice. Distrust of models seemed to grow later, perhaps in the 1970s or 1980s (H. Rozwadowski, pers. comm.).

1960–1980 Deterministic Theory, Statistical Practice. Between 1960 and 1980 the science of fisheries modeling solidified with contributions along a number of research fronts (i.e., surplus production, harvest theory, per recruit analyses, age-structured models, stock-recruit models, estimation of animal abundance). For the most part, the models were deterministic in character, in which the fundamental dynamics were described by fixed parameters that were constant in time. Advances in the statistics field were also being made and were transferred into fisheries through data analysis. But statistical theory had not developed sufficiently to allow complex models with stochastic elements for more realistic depiction of fish populations.

John Gulland. John Gulland was one of the most important fisheries scientists. He was a scientific leader with ICES, IWC and the Food and Agricultural Organization of the United Nations, and wrote and edited several books on fish stock assessment and fisheries management. Arguably his most important contribution was a mimeographed gray literature annex [1965] that showed how to modify Fry's VPA to allow for natural mortality. As such, an iterative, age-structured method for estimating abundance from catch data was available for the first time and became the main stock assessment method for ICES and around the world. The need for such a method came about within ICES and ICNAF because a primary responsibility of scientists was to develop a biologically justified catch limit, called the total allowable catch (TAC). The TAC was calculated as the product of the current biomass and a optimal exploitation rate such as the rate producing MSY (from Hjort, Thompson, Graham, Schaefer, and Chapman). The VPA method allowed the estimation of current biomass from catch-age data and chosen values for terminal fishing mortality and natural mortality. The TAC approach has been the primary means of attempting to control fishing mortality in most commercial fisheries up to the current time.

Gulland also led the way in establishing MSY as the dominant management strategy (with Chapman, Beverton, Holt, and others). Gulland enjoyed dealing with the intricacies of data analysis found in stock assessment, such as the analysis and standardization of catch-per-unit-effort (CPUE) data, and developed heuristic but quantitative approaches for analysis of fisheries data. Consequently, he wrote two books about fish stock assessment [1969, 1983] and edited others on fisheries population dynamics and management (e.g., Gulland [1988a]). He also wrote several perspectives on the role of science in management (e.g., Gulland [1978], [1988b]).

Surplus Production and Stock-Recruitment. Improvements to surplus production and stock-recruit models were made during this time. Chapman and his colleagues [1962] applied Schaefer's approach to Pacific halibut data and derived MSY quantities. The IWC Committees of Three and Four (Chapman, Allen, Holt, Gulland) successfully applied mathematical models to whale populations and showed that whale harvesting needed to be reduced. Pella and Tomlinson [1969] generalized the Graham-Schaefer production model by using a Richards function instead of the logistic. Allen [1971] developed the relationship between production and biomass for a year-class by combining alternative mortality and growth models. In particular, he showed that the ratio of production to biomass is equal to instantaneous total mortality Z, when the form of mortality is negative exponential and the growth model takes on several common forms. Schnute [1977] derived a nonequilibrium estimation approach for the Graham-Schaefer production model, making it possible to avoid the ad hoc and incorrect equilibrium approaches used in the past. Hilborn [1979] constructed a difference-equation form of the Graham-Schaefer model with similar effect. Fletcher [1978a,b] reparameterized the Graham-Schaefer and Pella-Tomlinson models and showed their phase-plane and temporal behavior. As mentioned previously, Cushing and Ricker had seminal publications on stock and recruitment. Larkin [1989] gives a historical overview of the development of scientific inquiry into the relationships between recruitment, spawning stock and the environment, singling out the publications of Ricker [1954] and Beverton and Holt [1957] as transcendent moments in that history.

Growth Models. Models for growth of individuals occur throughout the 20th century with major contributions by Brody [1945], von Bertalanffy [1938] and Richards [1959], along with Ricker and Beverton and Holt. By the 1970s, several alternative models had been developed and interest in formal parameter estimation techniques was beginning (see Quinn and Deriso [1999]). For example, Gallucci and Quinn [1979] showed how nonlinear least squares could be used to estimate the von Bertalanffy growth curve in better fashion than methods in practice at that time. Fletcher [1975] showed the correspondence between the models for growth of a population and for the growth of an individual.

Age-Structured Methods. A renaissance of age-based approaches and models occurred. Chapman and Robson [1960] put catch curve analysis, originally developed by Heincke and Baranov and others, on a statistical footing. Along with Gulland's [1965] VPA, variants were constructed by Jones, Murphy and others. John Pope made a major breakthrough in 1972 when he developed a noniterative method called cohort analysis as an alternative to VPA. Based on an approximation to the Baranov catch equation, it involves back calculation from the oldest age (say A) to the youngest age:

$$N_a = N_{a+1} \exp(M) + C_a \exp(M/2),$$

given values for natural mortality M and the terminal fishing mortality F_A. The beauty of cohort analysis is that the further the back calculation proceeds, the smaller the error becomes due to incorrect specification of F_A.

Doubleday [1976] constructed the first statistical formulation of catch-age analysis (based on some earlier work by Pope in 1974). A forward calculation method (Figure 6), it starts with initial recruitment N_r for each year-class and utilizes the following straightforward set of

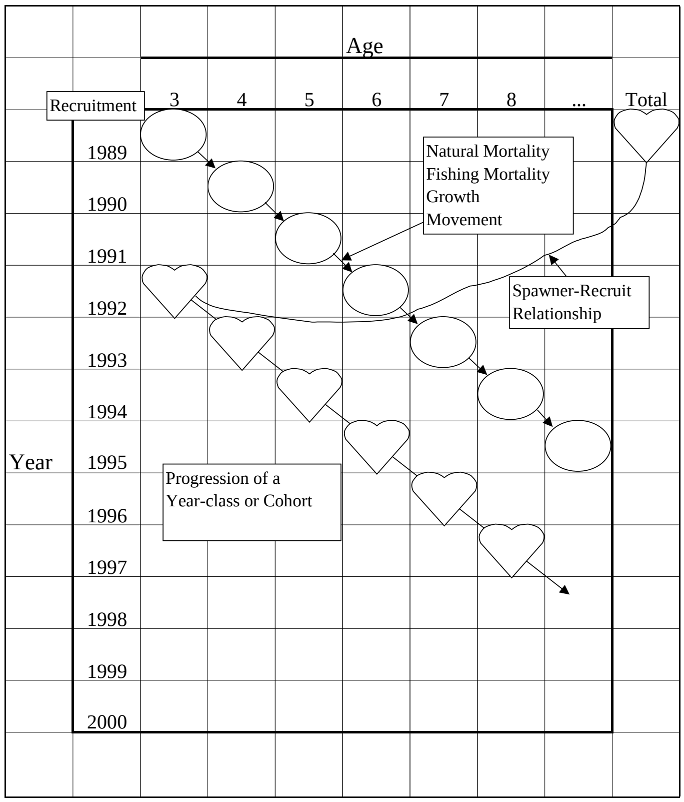

FIGURE 6. Operational modeling in age-structured models, as it appeared in Doubleday [1976], Fournier and Archibald [1982], Deriso et al. [1985], and later statistical age-structured assessment modeling.

equations:

$$N_{a+1} = N_a \exp[-(F+M)], \quad \text{the basic survival equation,}$$
$$C_a = N_a(F_a/Z_a)[1-\exp(-Z_a)], \quad \text{the Baranov catch equation,}$$
$$Z_a = M + (\text{selectivity}_a)\,(\text{fully-selective } F).$$

The last equation invokes the separability assumption in which fishing mortality is separated into an age-specific selectivity factor times a year-dependent fishing intensity. An objective function is set up which minimizes Σ(observed catch $-$ predicted catch)^2. Although he abandoned this approach because of poor performance, it later became the fundamental basis for age-structured stock assessment.

During this period, several applications of Leslie matrix models occurred in both fisheries and ecology (see Caswell [2000] and Quinn and Deriso [1999] for references).

Estimation of Animal Abundance. Mark-recapture, line-transect and catch-effort methods advanced during the 1960s and 1970s. Many of the methods published were independent of population processes (direct methods). The advantage was that no direct accounting of these processes was needed. On the other hand, it required stringent assumptions about population closure and/or catchability. The single most important advance was the publication of *Estimation of Animal Abundance* by George Seber in 1973 (with a second edition in 1982). This book was encyclopedic in its coverage and consequently standardized and advanced the field. Other significant contributors to these advances include: Arnason, Buckland, Burnham and Anderson and White, Chapman, Cormack, Eberhardt, Jolly, Manly, Pollock, Ricker and Robson. Of note for this discourse is the advent of the Jolly-Seber model in the 1960s because it included population processes: estimates of recruitment, mortality, abundance and the probability of capture could be made for each time period. However, in the field as a whole there was little integration of statistical methods and population dynamics.

Multispecies Models. After the pioneering work on multispecies models by Lotka and Volterra in the 1920s, there were few other advancements until the 1970s. Multispecies models returned to popularity thanks to large-scale ecosystem-type programs sponsored by the National Science Foundation, among others. In fisheries, Anderson and Ursin [1977] constructed an ecosystem model for the North Sea and used it to explore effects on the ecosystem from fishing and changes in fish populations. Similarly, Laevastu and Larkins [1981] developed a multispecies model of the Bering Sea which was used to develop a conceptual basis for the fishery management plans under the new North Pacific Fishery Management Council. These models required setting parameters for interactions among species and trophic levels for which little or no data existed. Among others, Robert May [1973] used information theory to demonstrate the unpredictability of these models because they have so many linkages with so little information. Eventually, the use of multispecies fish models for assessment and management ceased until the late 1990s. ICES had a multispecies working group and organized a major stomach sampling program for several years in the 1980s and 1990s. While many theoretical advances were made, a recurring theme was the inability to make multispecies models operational for stock assessment and management purposes (Rozwadowski [2002]).

Colin Clark. The integration of economic theory with population dynamics models intensified in the 1970s, particularly due to the efforts of Colin Clark. While there had been earlier efforts to blend economic and biological theories (e.g., by Graham, Beverton, and Holt), the separation between economists and biologists in most institutions meant that these efforts did not go far. Working at the University of British Columbia since 1960, Clark published his seminal paper "The Economics of Overexploitation" in *Science* in 1973, showing how economic pressure leads to overexploitation of natural resources in a common property environment. He developed models of depensation for whale and schooling populations, showing how population crashes could occur. He synthesized the blending of population dynamics with economic theory through the publication of *Mathematical Bioeconomics* in 1976 (2nd edition, 1990) and *Bioeconomic Modeling and Fisheries Management* in 1985. Clark's later work in the 1980s and 1990s concerned optimal strategies and decision-making for fisheries management in light of uncertainty. He and Marc Mangel collaborated on papers dealing with aggregation and search theory (e.g., Clark and Mangel [1979]). Mangel has emerged as one of the strong quantitative thinkers in ecology and natural resource issues (e.g., *The Ecological Detective* with Ray Hilborn in 1997).

1980–2000 The Golden Age. Attempting to describe the most recent period is an enormous challenge. The number of articles, books, authors and journals has increased greatly. I apologize to authors who deserve recognition in this article and who escape mention due to my oversight. History requires the passage of time to sift out the important work and contributions for a given time period; thus it may be premature for me to do so here. Furthermore, propinquity tends to overemphasize the familiar.

My contention is that a Golden Age existed between 1980 and 2000. The Golden Age occurred because of the explosion of quantitative papers in fisheries by a wider and wider group of scientists, the generality and generalizations of approaches used in the past, and most importantly, the integration of mathematics, computers, statistics and biology to an extent much greater than in the past. These models were used to formalize and standardize the scientific advice given to management agencies and to provide a framework for the understanding of disparate data and information sources. To counteract the major limitation that modeling is a reductionist activity, modeling during the Golden Age evolved to include more realistic assumptions and more complex descriptions of the population than ever before.

This proliferation of models has also been criticized in some circles, with the argument being made that too much attention is given to the modeling details and not enough to the requisite understanding of available data, of the biological and ecological framework and of uncertainties about the system and the data collected from it. Indeed, Hilborn [1992] spoofed stock assessment science as being a "special priesthood gather[ing] for their annual rites that affect lives of millions." Thus, the mistrust of modeling has been a constant presence in fisheries science.

Institutions. In the Golden Age institutions were established that advanced the development of quantitative approaches to fisheries study and management. For example, the formation of the Institute of Animal Resource Ecology at the University of British Columbia (with Holling, Larkin, Walters, and Hilborn) and the Center for Quantitative Science at the University of Washington (with Chapman, Gallucci, Fletcher, and Mathews) provided an academic environment for the exploration of new approaches. The partnership of Anderson, Burnham, and White (Utah State University, Colorado State University, U.S. Fish and Wildlife Service) led to major improvements in the estimation of animal abundance. International Commissions and Councils (for Pacific halibut, tropical tunas, Atlantic fisheries, ICES) provided organized bodies for research and discussion. The 200-mile limit brought fisheries home to many countries, with interest for the first time in some fish resources. In Alaska the oil pipeline provided new revenue for increasing state management and research. The Alaska Fisheries Science Center has put together one of the best cadres of stock assessment scientists in the world to fulfill its increasing responsibilities in groundfish management support. At the University of Rhode Island Saul Saila was a one-person fisheries science center. Under his auspices many of the leading stock assessment and fisheries scientists on the east coast of the United States got their start and learned new statistical and mathematical techniques. Now semi-retired, Saila remains a renaissance man who studied diverse literatures and incorporated their techniques into fisheries science.

Many state, federal and international agencies have expanded their data collection and research efforts (NRC [2000]). There is greater collection of length and age data according to sound sampling designs. Whereas much early research relied on statistics from the fishery, there is now a greater emphasis on research surveys and observer programs so that accurate indices of abundance and accurate accounting of removals due to harvesting can be obtained. Because of technological advances and changes in fishing behavior, the catch per unit of effort from the fishery may not be a good index of abundance. Conversely, many harvesters are now more suspicious of agency stock assessments because their data and perceptions are not being incorporated in many cases and because they do not understand the complex models being used. A case study that illustrates the tension between scientists and user groups is the groundfish fishery in the Northeastern United States (NRC [1998b]).

During the Golden Age, cross-fertilization of quantitative ideas occurred internationally within the traditional venues (*Canadian Journal of Fisheries and Ocean Sciences*, *ICES Journal of Marine Science*, *Transactions of the American Fisheries Society*) and new journals (for example, *Fisheries Research*, *North American Journal of Fisheries Management*, *Reviews in Fish Biology and Fisheries*). Participation by the United States and Canada in ICES meant that new approaches would be recognized across North America. While there remained regionalism in preferred approaches, there was no other time period when scientific discoveries were as pervasive across the world. Advances in technology such as FAX and the Internet also meant that interchange could occur more quickly and effectively than at any other time.

Major Advances. Except for specific papers I wish to single out, I will generally refer to general topics with a list of authors. The specific references can be found in the references heretofore mentioned, particularly Hilborn [1992], Hilborn and Walters [1992], Funk et al. [1998], Quinn and Deriso [1999] and Quinn [2002].

Many authors developed nonlinear, statistical and stochastic models for catch and effort. In particular, Mangel and Clark [1986] employed search theory to show how proper indices of fishing effort utilize the time spent searching for fish schools. Nonequilibrium methods for surplus production were developed and synthesized into a general-purpose computer program, ASPIC, that is widely used (Prager [1994]).

Spawner-recruit models were formulated with measurement and process error in a collection of three papers (Walters, Ludwig, A. Smith, [1981]). They showed that the understanding of spawner-recruit relationships could be masked by measurement error, and developed methods for teasing out the different sources of error. Later work by Walters [1990] showed that the autocorrelated nature of spawner-recruit data leads to bias in estimated parameters, which can be corrected for. Kalman filter methods have been developed to deal with both measurement and process error (Pella [1993]). Spawner-recruit models for semelparous populations were used to evaluate constant escapement policies (e.g., Hilborn [1979], Walters [1981]). The constant escapement policy used for Alaska salmon is thought to be a major reason for the health of its populations (Eggers [1993]). Peterman and his colleagues at Simon Fraser University have made several advances in the understanding and modeling of Pacific salmon populations. Alternative spawner-recruit models were developed by several researchers (e.g., Deriso, Shepherd, Thompson).

Returning to the theme of the role of the environment versus other factors in explaining recruitment and population change, we see there has been a major research effort to assemble environmental data sets and relate them to fish populations (Wooster, Hollowed, Mantua, Beamish, Hare, Francis, Peterman, among others; see Beamish and McFarlane [1995]). Environmental relationships with recruitment in spawner-recruit models have been developed and applied with some success. The discovery of regime shifts in the environment has complicated fisheries assessment and management. If there are long time periods when population parameters are changed due to the environment, how does one detect the change and alter assessment and management (Walters and Parma [1996], NRC [1998a])?

Growth models have been generalized and reliable statistical estimation methods developed (Schnute [1981] and many others). Sainsbury [1980] showed that individual variation in growth can lead to estimation bias in traditional growth models. Francis [1988] showed that length-age data and mark-recapture data on growth are not strictly comparable. Stochastic growth models have been widely used, particularly in length-based models (see below).

A new class called delay-difference models emerged during the Golden Age. Although there was some earlier work with abundance of whales with a lagged recruitment term by Allen and C. Clark before 1980 (Quinn and Deriso [1999, Section 5.1]), the major advance for fisheries was the paper by Deriso [1980]. Using a difference form of the von Bertalanffy model (with growth parameter κ) for the weight of individuals in an age-structured model [$W_a = (1+\rho)W_{a-1} - \rho W_{a-2}$, with $\rho = \exp(-\kappa)$], Deriso developed the following recursion equation for the biomass B of a population:

$$B_{t+1} = (1+\rho)lS_t - \rho l^2(S_t/B_t)S_{t-1} + R(S_{t+1-r}),$$
$$\text{with} \quad l = \exp(-M),\ S_t = B_t - Y_t,$$

Y = yield, R = spawner-recruit function and r = time lag between spawning and recruitment. This equation shows that future biomass is the summation of the surviving biomass after fishing and adjustment for growth, a nonlinear correction term for growth and new additions to the population from recruitment. The most notable features of this model are that it derives from the biological realism of an age-structured model with a time delay for recruitment and it can be fitted to nonage-structured data. The elegance of Deriso's model prompted Carl Walters [1980] to write that this paper "may be the most important contribution to fisheries population theory in the last two decades." Schnute [1985] generalized Deriso's model and there have been other developments by Kimura, Walters, Quinn, Collie, and Pella, among others. This class allows the exploration of theoretical features of age-structured populations (such as equilibrium solutions and stability) in a simplified setting. An elegant construct has unified production, depletion, delay-difference and age-structured models (Xiao [2000]).

Two further advances in age-structured approaches involve per recruit models and Leslie matrices. Generic per recruit models, more flexible than the Beverton-Holt model, have been developed (Quinn and Deriso [1999, Chapter 6]). These models usually use a difference-equation form that is easier to calculate and can practically be used with any type of growth model, selectivity function or maturity/fecundity schedule. These models have greatly aided the development of catch limits and harvest management strategies. In a landmark paper, Sissenwine and Shepherd [1987] showed the interconnections among production, dynamic pool (per recruit) and spawner-recruit models, and moved fisheries management control rules from maximizing yield to preserving spawning biomass (see below).

There have also been substantial enhancements and extensions to Leslie matrix models (Caswell [2000], Getz and Haight [1989], Quinn and Deriso [1999, Chapter 7] and many others). These include time-varying Leslie matrices, stochastic matrices and nonlinear matrices. As such, the Leslie matrix has been fully generalized to deal with age-structured, length-structured, spatial-structured (migratory) and stochastic populations (see below). This means that within a single species framework, all of the principal biological factors affecting a fish population can be incorporated into a realistic population model.

Integrated Stock Assessment Models (*CAGEAN, Stock Synthesis, ADMB, ADAPT*). One of the major developments in the Golden Age has been the development of sophisticated age-structured models for stock assessment. In western North America these models have evolved from Doubleday's earlier approach with catch-age data combined with auxiliary information. Fournier and Archibald used a likelihood formulation in 1982 in which a statistical model of the data is explicitly developed as a function of population parameters. The parameters are estimated by maximizing this likelihood of the data. Deriso, Quinn and Neal used a least squares formulation in 1985 which involves the squared differences between observed quantities and corresponding model predictions. Deriso et al. provided perhaps the earliest applications of bootstrapping (to estimate variance) and retrospective analysis (to determine bias, see below) in the fisheries literature and a computer program, CAGEAN.

The inclusion of auxiliary information along with catch-age data allows for unbiased estimation. Examples of such information include survey age composition, survey abundance and biomass (whether relative or absolute), spawner-recruit relationships, CPUE and effort, an index of recruitment, and direct estimates of abundance from mark-recapture or line transect methods. Additional useful developments of this approach have been made by Megrey [1989], Kimura [1990] and Methot [1990] (who developed a versatile computer program called Stock Synthesis), Fournier (who developed a flexible general purpose modeling program, AD Model Builder), Schnute and Richards, Myers, Ianelli, and McAllister, among others.

The general approach is to use equations that proceed forward in time with fundamental population parameters for recruitment, fishing mortality, selectivity and catchability (Figure 6). Usually, fishing mortality by age and year is assumed to be separable into age-specific (selectivity) and year-specific (fishing intensity) factors, in order to reduce the number of parameters to be estimated. Uncertainty in all data sources is accounted for by statistical modeling. An objective function relating the observations to the model is specified, from which parameter estimates are obtained. The resulting model can have thousands of observations and hundreds of parameters.

Consequently, this model development has no parallel in the statistics literature. The complexity and nonlinearity of the model structure, the large size of the problem and the presence of multiple data sets bring out statistical problems not regularly encountered in the field of statistics. In particular, there are issues involving the weighting of different information sources, conflicts among the different sources, the estimability of parameters and optimal model complexity.

In eastern North America and the ICES arena, the development of assessment models has evolved differently, following a line from Gulland's VPA and Pope's cohort analysis. Different implementations have been developed, starting with ad hoc tuning procedures that adjusted terminal fishing mortality inputs with the use of survey indices of abundance. The ADAPT method and computer program of Gavaris and others evolved in the late 1980s. ADAPT was a major advance over previous methods and is now the one most used in the eastern and western Atlantic. Here one uses equations that proceed backward in time, given terminal fishing mortality and natural mortality. Uncertainty in survey indices is accounted for by statistical modeling, but catch-age is assumed to be measured without error. An objective function relating the survey observations to the model is specified, from which parameter estimates are obtained. While the number of parameters estimated from the objective function is low, the actual number of parameters in the model is very large because there is a fishing mortality parameter for each age and year. The major contributors to this approach include Pope, Shepherd, Laurec, Gavaris, Powers, and Conser.

Length-Based Models. Length and size composition information is a fundamental part of most data collection systems in fisheries. It is relatively easy to measure a large number of fish in the catch or in a survey, and the modal patterns in their frequency distributions should be indicative of the relative abundance of year-classes. The conversion of length to age can be problematic due to vagaries in growth patterns, and few length-based models existed in 1980. During the Golden Age, rigorous length-based assessment models came into their own. Beddington and Cooke [1981] developed one of the first rigorous length-based models. Pauly and Morgan [1987] edited a book on length-based approaches. Deriso and Parma [1988] derived an age- and length-based stochastic model which was extended by Quinn and his colleagues. Fournier made several contributions to length-based methods which has resulted in a useful computer program, MULTIFAN. Schnute and his colleagues developed a general approach with delay-difference models and stochastic growth. Methot [1990] adapted Stock Synthesis for length data, with age-based dynamics and deterministic growth. Sullivan, Lai and Gallucci [1990] constructed a length-based model by adding stochastic growth to the Deriso et al. [1985] catch-age model. Caswell [2000] and Getz and Haight [1989] describe extensions to the Leslie matrix; these extensions replace age with life history stage or length classes. Several other important advances are detailed in Quinn and Deriso [1999, Chapter 9]. Consequently, the skepticism about length-based models as mentioned in Hilborn and Walters [1992], and which I shared at the time, has diminished substantially.

Spatial Dynamics. Most fish exhibit movement and migration (patterned movement) at some phase of their history. Even if such movement is minor, there is now increased interest in the smaller-scale patterns of fish populations and local depletion effects of fisheries. Spatial considerations have occurred throughout the history of fisheries science (e.g., Beverton and Holt [1957]), but it has really only been in the last twenty years that spatial models have emerged. Hilborn, Schwarz, and Burnham, Anderson and White have developed new methods of estimating movement from recaptures of marked or tagged animals. Spatial dynamics have been explored by a variety of authors (see Quinn and Deriso [1999, Chapter 10]). Caswell [2000] and Heifetz and Quinn [1998] considered extensions to the Leslie matrix. Deriso and his colleagues developed a stochastic, nonage-structured model for tuna. MacCall [1990] developed a basin model to represent habitat suitability and its impact on population dynamics. Quinn, Deriso and Neal [1990a] extended catch-age analysis to migratory populations. Pelletier and Parma [1994] examined spatially explicit models for Pacific halibut using geostatistical techniques. Run reconstruction models for returning salmon populations have been developed by Schnute and Sibert, Starr and Hilborn, Mundy, Templin, Collie, and Quinn, and Su and Adkison. Habitat based models have been developed by Polachek, Botsford, and Fujioka among others.

Estimation of Animal Abundance. There have been continual improvements to methods during the Golden Age, most of which are summarized in reviews by Seber and Schwarz ([1986, 1992, 1999]); see Schwarz and Seber [1999]) and Buckland et al. [2000]. Line transect theory is carefully summarized in Buckland et al. [2001]. In mark-recapture, the trend has been to develop flexible modeling of population processes and capture probabilities. As such, the population dynamics has become fully integrated with the statistical methodology. There has been a convergence of modeling philosophy in the fisheries (e.g., Hilborn, Schwarz) and the ecological literature (e.g., Anderson, Burnham, White, Pollock), although this convergence is not yet widely recognized by either group. A variety of computer programs (MARK, SURVIV, SPAS) are available.

Bayesian Methods and Accounting for Uncertainty. The development of Bayesian methods and numerical approaches for using them is perhaps the most significant and obvious (from the large number of publications) advance during the Golden Age. This use of Bayesian methods is now pervasive in all fields of statistics and natural resources. Geiger and Koenings [1991] and Walters and Ludwig [1994] were two of the first papers to utilize Bayesian methods in fisheries; excellent overviews of the approach are by Punt and Hilborn [1997] and Francis and Shotten [1997]. Hilborn [1992] predicted correctly that Bayesian methods would be the future of stock assessment. He referenced first efforts by Fried and Hilborn with Pacific salmon, Sainsbury with Australian fisheries, and Raftery et al. with whales, all published in 1988. Some of the other people who have contributed to this advance in fisheries are Fournier, McAllister, Pikitch, Ianelli, Adkison, and Peterman. Some applications include analysis of spawner and recruit information, models of the fishing process, delay-difference models, estimation of age and size composition, age- and size-structured models, decision analysis of harvesting policies, sampling design and the estimation of animal abundance (mark-recapture, line transect).

The Bayesian approach builds on the likelihood approach by allowing some parameters to be random variables with distributions called priors. The prior distribution of a parameter is updated by the data through the likelihood to produce the posterior distribution of the parameter. It used to be nearly impossible to conduct a Bayesian analysis except in the simplest cases with particular distributions, because of the need to conduct integration over several variables. But now several Monte Carlo algorithms (e.g., MCMC) exist to allow numerical solutions for the problems most people want to solve.

The Bayesian formulation allows explicit specification of uncertainty through the prior distribution, and has been used to include perceptions and information for which it is difficult to develop likelihoods. At one time one had to ascribe to a particular belief system to undertake Bayesian analysis, but now the stigma associated with Bayesian analyses has largely disappeared. The focus has shifted from "belief systems" to enlarging the toolbox. There now exists a suite of uncertainty measures (credibility intervals), measures of model fit (e.g., Bayes factors) and sensitivity study approaches to judge the influence of underlying assumptions. Nevertheless, results do depend on choice of the prior distribution (Adkison, Peterman), which can lead to controversy. There have also been attempts to use alternative bootstrap, likelihood and fuzzy arithmetic approaches to deal with uncertainty (Cordue, Ferson, Saila).

Times Series Analysis. By and large fisheries modeling has either been deterministic or its statistical models have assumed independent and identically distributed errors. In reality we expect that there is autocorrelation over time and space due to environmental and physical reasons. One approach for dealing with autocorrelation has been widely used: forecasting with the Box-Jenkins method (several authors). Structural models that combine population dynamics with autocorrelated error processes have been less widely considered but have much merit (Gudmundsson [1994], Criddle and Havenner, Fournier, Ianelli, Myers). In particular, the AD Model Builder program allows for random walk models for population parameters in nonlinear models. For example, it may be true that natural mortality is equal to what it was last year plus a random error. Such time series processes allow explicit specification of uncertainty like Bayesian methods do. Failure to account for these autocorrelations leads to errors in stock assessments (Walters [1990], Myers and Cadigan [1995]).

Retrospective Analysis. Retrospective analysis is the comparison of results from models or data, when one year of data is removed at a time (Deriso, Quinn and Neal [1985], Parma [1993], NRC [1998a]). While researchers have conducted such analyses for several years, there has been little supporting theory to interpret what is seen. Patterns of large differences in a parameter (say, recruitment at age 2 in 1998) can occur due to model misspecification, estimability problems or variability in the data. Consequently, retrospective analysis can help identify problems with a stock assessment.

Meta-Analysis. Meta-analysis is the amassing of data and parameters from several fish populations, and the examination of similarities and differences among groups such as fish stocks, species or trophic levels. One of the first examples of meta-analysis is the attempt to develop predictive equations for natural mortality. The work of Pauly [1980] is the best known, but Alverson and Carney, Hoenig, and Gunderson have also obtained useful results. Myers and his colleagues at Dalhousie University have been responsible for major advances in meta-analysis by collecting data on spawner-recruit data sets and other population parameters. In Myers et al. [1995], these data sets were re-analyzed to explore whether depensation (inability of a population to recover at a low population size due to depressed early life survival) could be detected. They showed that it did not appear to be found in most data sets, which means that attempts to rebuild depleted stocks by reducing exploitation are feasible. Meta-analysis has many potential uses. It may allow population parameters to be "borrowed" for stocks with little or no information. In Bayesian analyses, such information could be used to construct prior distributions. The collective examination of multiple data sets may allow significant results to be obtained (from random effects analysis, for example) where previous individual analyses were unable to show any effect.

Evaluation of Assessment Models. There have been two major evaluations of stock assessment models in the past. The first was conducted under the auspices of the Methods Working Group of ICES in the late 1980s and organized by G. Stefansson and D. Armstrong (ICES [1993]). Scientists were invited from around the world to try their methods on blinded, simulated data from known populations. The goal of the evaluation was to establish a procedure by which new methodology could be evaluated before being presented to other working groups (i.e., certified by simulation testing). The results showed that many of the newer methods did not out-compete the earlier ones and that statistical models (like CAGEAN and time series analysis of catch-age data) generally out-competed more ad hoc approaches in accuracy. However, they were also more time-consuming.

The second evaluation was conducted under the auspices of the National Research Council of the U.S. National Academy of Sciences (NRC [1998a]). Similarly, blinded simulation data sets were constructed and given to teams of U.S. scientists, primarily from the National Marine Fisheries Service. This exercise provided a sobering view of the inability to estimate population parameters well under some realistic conditions. There was also a suggestion that more complex models had the flexibility to perform better, although not uniformly so.

Modeling Philosophy. In summary, the Golden Age has resulted in major advances in population dynamics models, the treatment of uncertainty, and the integration of biology, statistics, and mathematics, and the comprehensive analysis of multiple data sets. The resultant modeling philosophy is shown in Figure 7. The ability to combine

Model Component	**How uncertainty is incorporated**
Population Dynamics Model	Stochastic parameters Time-series parameters Prior distributions for parameters Alternative models
Observation Model	Equations to relate observations to the model Statistical models for uncertainty
Objective Function	Sums of squares and likelihoods Weightings for individual components and data Perceptions Robust likelihoods Treatment of outliers Bayesian model Shrinkage estimators
Outputs	Parameter estimates and confidence intervals Forecasts Bootstrap statistics Posterior distributions Decision tables for competing models and management actions

FIGURE 7. Summary of the current philosophy of fisheries modeling.

population dynamics with uncertainties in data and parameters in a statistical setting is evidence that the study of population dynamics has become a mature science. The rigor and breadth of the field is impressive, astounding and unique.

Population Dynamics and Fisheries Management. It is beyond the scope of this review of fisheries models also to review all of their uses in fisheries management. But it is important to recognize that the advances in fisheries models have had direct and complementary effects on fisheries management philosophy and practice (Quinn and Collie [in press]). More comprehensive coverage of quantitative techniques in fisheries management can be found in Kruse et al. [1993], Smith et al. [1993] and the proceedings of a conference on uncertainty in fisheries management (ICES Journal of Marine Science, vol. 56). In addition, Rozwadowski [2002] describes how the process of providing scientific advice evolved within ICES, leading to management based on limits of total allowable catches (TACs) recommended by working groups. This activity occupied a major part of the ICES system in the 1960s through the 1980s, leading many to question whether proper attention was being given to basic scientific questions.

Above all, fisheries management has become more conservative and precautionary. The theory underlying maximum sustainable yield (MSY) is fully developed and applicable to spawner-recruit models for semelparous populations (in which individuals make a single reproductive contribution at the end of life), surplus production models, delay-difference models, and age- and size-structured models (Getz and Haight [1989], Hilborn and Walters [1992], Quinn and Deriso [1999]). Despite Larkin's [1977] epitaph to MSY, it is alive and well in the new millennium. However, MSY has become a limit rather than a target, as scientists have realized that stochasticity, uncertainty, management error and biological processes can all interact to prevent the attainment of MSY. Much of this realization has come from complex computer simulation models with stochastic elements.

There has been recognition of the difficulties in determining MSY for populations with no clear spawner-recruit relationship and with high recruitment variability. As time has passed, more focus has been placed on biological reference points (BRPs, usually expressed as fishing mortality values) on a per recruit basis, as thoroughly presented in Beverton and Holt [1957]. The first of these was $F_{\max}$, the fishing mortality that maximizes yield per recruit (for a given selectivity or partial recruitment schedule). Fletcher [1987] extended the theory of the Beverton-Holt model for maximizing yield per recruit and related problems. Because $F_{\max}$ does not include compensation that is included in a spawner-recruit relationship, it frequently produces values that are larger than F_{msy}. Because of that, it was eventually eliminated as a BRP for setting quotas.

Colleagues at ICES and ICNAF developed the alternative of $F_{0.1}$ in the 1980s (Anthony [1982]). This BRP is the fishing mortality for which the marginal increase (slope) in yield per recruit is 10% of that with no fishing. Deriso [1987] developed the theory for this reference point and its relationship to the Beverton-Holt theory. The major problem with $F_{0.1}$ is that it does not contain an explicit recognition of the preservation of spawning biomass and reproductive value.

As mentioned earlier, Sissenwine and Shepherd [1987] showed the linkages between spawner-recruit (reproduction), yield-fishing mortality (production) and per recruit (dynamic pool) relationships for yield and spawning stock. Their interest was in developing new BRPs that dealt directly with recruitment overfishing and maintaining spawning biomass and reproductive potential. In the 1990s this goal was made operational by the expanding use of a new BRP $F_{x\%}$, the fishing mortality that reduces spawning biomass per recruit to $x\%$ of the value under no fishing (i.e., the pristine per-recruit population). This change occurred due to many scientific studies during this period, including W. Clark [1991], Mace and Sissenwine [1993] and Thompson [1993]. Clark's work was particularly important, as it showed that under a variety of typical life history parameters and spawner-recruit relationships, a suitable proxy for MSY is $F_{35\%}$ for stocks with typical productivity. Further studies have also explored recruitment variability, depensation and a variety of actual populations, and have led to a more conservative recommendation of $F_{40\%}$ as the maximum permissible fishing mortality for many stocks. Further conservatism has been included in fisheries management by the consideration of control rules that reduce fishing mortality if a population drops to low levels. One example of this approach is threshold management (Quinn et al. [1990b]) in which fishing ceases if the population drops below a set threshold value.

Perhaps no topic in fisheries management has been more discussed over the last 20 years than adaptive and experimental management, as pioneered by Walters [1986] with additional contributions by Collie, Hilborn, Peterman, Sainsbury, and Smith, among others. Adaptive management seeks out optimal harvesting policies by learning from the information collected and changing the management strategy accordingly. Mathematically, this approach requires complicated algorithms from the field of dynamic programming.

Another major advance in fisheries management has been the development of robust management procedures based on thorough simulation testing with operating models (Butterworth et al. [1997], Cooke

[1999], Punt). In this approach, all reasonable hypotheses regarding the states of nature affecting the population are considered. An operating model that characterizes the essential data collection and assessment, usually simplified to allow sufficient computer simulation testing, represents the assessment mechanism. The goal is to find a harvest policy that avoids risk to the population no matter which processes affect the population.

This history of fisheries models has shown that one of the prevailing controversies has been whether the fishery or the environment has a bigger role in the fate of exploited populations. A further question is how management strategies should be designed in the presence of environmental changes (NRC [1998a]). It seems clear that the uncertainty induced by climate change should lead to increased conservatism in fisheries management. Walters, Parma, Collie, Deriso, and Peterman, among others, have done work in this area which is likely to be a research priority in the future (NRC [1998a]).

The New Millenium – Devolution. The incredible evolution in fisheries models foretells a future in which models will handle thousands of observations from any number of data sets with hundreds of parameters. And computer hardware and software will be available to handle these complex models. The models will deal with uncertainty properly by including measurement, process and model specification errors.

Clouds on the Horizon. All the same, greater demands will be placed on models to answer complex questions. It is unlikely that all questions will be resolved because some questions will simply not be resolvable with finite resources. Even now data needs often overwhelm the performance of models. For example, simulation studies show that there can be huge biases in stock assessments (ICES, NRC studies). For example, one simulation exercise from NRC [1998a, Figure I.3] shows that the most recent exploitable biomasses are overestimated by all assessments, which include state-of-the art techniques. The lesson is not that assessment science is flawed, but rather that good assessments cannot be done without quality information and understanding of biological and fishery processes.

Perhaps there has never been a time when the reputation of fisheries management has been so poor. The public's perception of fisheries is that they are mismanaged and that all stocks are in trouble, when in reality many stocks are well managed and healthy. The view of many regarding U.S. Fishery Management Councils is that the foxes are in charge of the henhouse, whereas many responsible decisions have been made (and many irresponsible ones too). By implication, the science that has supported fisheries management has been called into question as well, despite the advances that have been described in this paper. On the other side, resource users often feel that there is a disconnect between modeling results and their perceptions of the health of a population. Often this is due to statistics from the fishery being more favorable about population health than survey statistics. All the same, there have been many situations in which resource users feel that their information is not being used, and scientists feel that the fishery data is suspect and/or biased. Bridging these gaps in communication seems like a hopeless task at times.

At the same time, there seems to be a major lack of understanding about the fundamentals of population dynamics and interrelationships among species. This has led to fisheries models being attacked for being a "single-species approach" that does not protect the ecosystem. Calls to replace existing science and management with new holistic paradigms rarely offer much detail. Inherent in many attacks is a basic misunderstanding of sustainability (Quinn and Collie [in press]). Part of this problem traces to the continued separation of ecologists and fishery scientists. At times it seems that there is lack of a common language and a common currency for substantive exchange.

There seems to be a basic misunderstanding of carrying capacity. Cumulative changes in reproductive parameters, juvenile and adult survival, growth, prey availability and predator populations may all contribute to changes in carrying capacity over time, yet many still view this parameter as a constant value. Human activities may contribute to the changes in population parameters, and hence to fluctuating carrying capacity, but this effect has been difficult to quantify.

There is an increasing tendency to engage in conservation one-upmanship: "Your models do not explicitly account for factor x; therefore, you should be 'precautionary' and reduce the quota by y." "Your management strategy is to deliberately reduce populations by fishing them." Type II error (not taking action when a problem is occurring), the focus of precautionary management, is taking precedence over Type I error (taking action when no problem is occurring), the focus of traditional management. Hence, the burden of proof is shifting from not intervening in a human activity until harm can be proved, to requiring proof that an activity is not having an undesirable effect. While this has been a positive and proactive development, the question of balancing Type I and Type II error has not been resolved.

Because of the pressure from the scientific community and the public to make fisheries management more of an ecosystem approach (NRC [1999]), I predict that funding will shift from single-species assessments to other lines of inquiry. This is why I believe that the Golden Age of Fisheries Models is over (Figure 1). Instead, there will be many "feel-good" studies that promote views of a harmonious world where needs of all species are properly balanced and *Homo sapiens* learn their proper place in the ecosystem. There will be increased reliance on perceptions and anecdotal information so that *all individuals* feel empowered by having their viewpoints represented.

Already there has been a renaissance of ecosystem models which carry many of the same limitations as those from the 1970s. Yet there are calls to replace rigorous population dynamics models with these ecosystem models which have limited predictive capability. Consequently, I predict that these alternative models, if they replace previous models, will be inferior to the single-species approaches and lead to substantial management errors and socioeconomic consequences. Finally, it is clear that the prevailing direction of change for fisheries management is to become more conservative. Therefore, fisheries will continue to be curtailed and in some cases will no longer be viable, creating drastic social and economic consequences for some sectors and communities reliant on fishing.

New Directions. The main purpose of this paper has been to show that fisheries modeling has advanced to the stage of a mature science. Nevertheless, there are many directions in which improvements can be made in the future. Habitat and spatial concerns have become more prominent, meaning that advances in spatial assessments are needed. There has been only minor consideration of population genetics in population dynamics models. The advances in DNA techniques make it possible to follow genetic families and diversity, if the proper theory combining population genetics and dynamics can be developed.

The desire to understand multispecies interactions will continue. In fisheries models, multispecies interactions have been represented by variations in natural mortality and recruitment, as well as in the Lotka-Volterra and ecosystem models. I hope that we don't simply repeat the past but develop models that are compatible with information sources. I contend that data needs for complete multispecies models will remain beyond human attainment. There are hundreds of potential interactions among species in an ecosystem, and these probably change over the year and between years. To totally measure species interactions, one would have to collect predation and competition data year-round over several years.

One of the key issues that must be addressed is understanding the effects of harvesting on the ecosystem. The Ecopath/Ecosim approach, a multispecies approach based on the flow of production through a system of species, has been used in this regard. Another approach, used in the North Pacific Fishery Management Council Supplemental Environmental Impact Statement analysis, is to utilize single species assessments within a multispecies management simulation.

The issue of whether harvesting or environment drives the dynamics of fish populations will continue to be controversial. It will be important for future fisheries models to include variation in both natural mortality and recruitment and to relate this variation to other time series. The incorporation of time series models within fisheries models should lend further insight into this problem.

The issue of model misspecification needs more formal treatment. We can now handle measurement error (in observations) and process error (stochasticity in population processes), but we don't know how to deal with model uncertainty and error very well. Bayesian methods and operating models may help to address this issue.

Finally, further advances are needed to address socioeconomic concerns using bioeconomic models. These models need harvester response and economic data collection and modeling, which has often been limited by confidentiality concerns. But useful predictions of economic and social consequences can only occur if the costs of harvesting are known as well as revenues.

I wonder what things will be like 50 or 100 years from now. Will the names of Baranov, Beverton and Holt, and Ricker still be known? Will fisheries models resemble those of today or be replaced by something totally different? Will there still be natural stocks of fish to manage and humans to manage them? No matter what happens, I hope that science, modeling and humans will have a role to play.

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