A review of harvest theory and applications of optimal control theory in fisheries management[1,2]

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Optimal control theory is a useful tool for analysis of general mathematical models of fisheries and harvest strategies. It provides a framework for management decisions, but is too general for direct application to many specific management problems. A review of applications of optimal control theory to fisheries management is presented, with a general audience in mind. Advantages and shortcomings of optimal control theory in the context of fisheries management are discussed with some specific examples.

La théorie du contrôle optimal constitue un outil utile pour l'analyse de modèles mathématiques généraux des pêches et des stratégies d'exploitation. Elle fournit une base pour les décisions relatives à la gestion mais elle est trop générale pour être appliquée directement à de nombreux problèmes de gestion déterminés. L'auteur présente, à l'intention du public, un examen des applications de cette théorie à la gestion halieutique. Il illustre à l'aide d'exemples ses avantages et ses inconvénients dans le contexte de la gestion halieutique.

The following is a review of some results from the applications of optimal control theory to fisheries management. Since the intended audience is broad, I tried, wherever possible, to keep the presentation at an introductory level, limiting the discussion to analytical models only, and pointing out some useful results and pitfalls. One needs to keep in mind that most analytical models are gross simplifications of reality. Thus, they are useful for general understanding of dynamics of overriding importance in systems. The usefulness of analytical models to *specific* management problems is limited mostly to qualitative rather than quantitative insights.

The General Optimal Control Problem

Optimal control problems in ecology arise in cases where the conditions are complex: multiple input–output; constraints on state, input, and control variables; stochastic systems with potentially time varying parameters; large-scale systems with time delays; complications introduced by unknown "observer" effects; and distributed parameter systems. Derivations of optimal control policies from analytical models are based on the presumption that the simplified models capture some overriding mechanisms which govern the system. This often requires a leap of faith.

The starting point in formulating an optimal control problem is the first-order differential equations (distributed systems are discussed briefly later):

(1) $dx_i(t)/dt = f_i[x_1(t), \ldots, x_n(t), u_1(t), \ldots, u_r(t)]$;

$$i = 1, \ldots, n.$$

In vector notation, (1) becomes

$$dx/dt = f[x(t), u(t)]$$

where $x(t)$ is an $n \times 1$ vector, representing the state of the system (e.g. species density), $u(t)$ is an $r \times 1$ input or control vector (e.g. harvest quota or harvest rate), and f is a vector-valued function. With time delays T, we have

(2) $dx(t)/dt = f[x(t - T), u(t - T)]$,

and for discrete systems,

(3) $x(k + 1) = f[x(k), u(k)]$

where k is the kth time interval.

The optimal control problem is stated as follows: Given the state eq. (1), a set of boundary conditions on the state variables at the initial and terminal times, and a set of constraints on the state and control variables, determine the admissible controls $u(t)$ so that a performance index (cost function) is minimized (or maximized). The boundary conditions are given by $x(t_0)$ and $S[x(t_f)]$ where t_0, t_f, and S denote, respectively, the initial time, the final time, and the target set. Note that t_0 is always fixed, but t_f may be part of the optimal control problem; e.g. one may strive to minimize t_f.

The performance index is expressed as a scalar quantity

(4) $I = G[x(t_f), t_f] + \int_{t_0}^{t_f} F[x(t), u(t), t]dt$

where G and F are scalar-valued functions.

The main theoretical approaches to the optimal-control-

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system design utilize calculus of variation (Luenberger 1969; Clark 1976a), the maximum principle (Pontryagin et al. 1962; Athans and Falb 1966), dynamic programming (Bellman 1957; Larson 1968; Walters 1975; Walters and Hilborn 1976), and mathematical programming (Canon et al. 1970; Tabak and Kuo 1971). But for the simplest problems, analytical solutions by calculus of variation are unobtainable, and numerical solutions are considered most difficult.

The maximum principle, like the calculus of variation, leads to both analytical and numerical difficulties. Dynamic programming is an attractive alternative (Walters 1975; Walters and Hilborn 1976), but requires excessive computer memory (Bellman 1957; Larson 1968) and is applicable to small systems, with few variables only. Because of the ease with which mathematical programming deals with inequality constraints and small computer memory requirements, it is perhaps the most attractive method of solving optimal control problems, especially those that are nonlinear and which involve large systems. Yet, this method presents difficulties when nonlinear nonconvex functions are involved (Tabak and Kuo 1971). It also suffers from disadvantages similar to simulations in that general conclusions are often difficult to derive and problem solutions are specific.

Single-Species Models

The theory of optimal harvesting of single-species populations is well developed, and solutions exist for models such as the logistic (Goh 1969–70; Clark 1973; Cliff and Vincent 1973; Gopalsamy 1980), the stock–recruitment model for nonoverlapping generations (Moran 1950; Ricker 1954; Hassell 1975; Goh and Agnew 1978), the Beverton–Holt model (Beverton and Holt 1957), fisheries with limited season (Clark 1976a; Goh 1980a), and fisheries with delayed recruitment (Clark 1976b).

Continuous Models

Essentially, all continuous single-species models are of the form (1) or (2). When the control variable is linear in the objective function and the system dynamics, as may happen in many ecological control problems (Goh 1969–70; Cliff and Vincent 1973; Goh et al. 1974; Clark 1976a; Wickwire 1977; Clark et al. 1979), the optimal control solution is either bang-bang or singular. Bang-bang control refers to an optimal solution which dictates that the control switches between two values only: its maximum or its minimum. Singular control arises when the optimization criterion equals zero (for further details refer, for example, to Lee and Markus 1967; Clark 1976a). Using the generalized Legendre conditions, Goh (1966a, 1966b) derived the set of necessary conditions for singular control, which was also discussed by Clark (1976a).

Optimal control solutions usually consider a planning time horizon which might be finite or infinite. To test for long-term optimality, the focal point condition must be satisfied (Bliss 1946; Goh 1966a). When optimizing with the time horizon infinite, the integral objective function (4) becomes infinite. To overcome this problem, (1) a discount factor may be introduced (Clark 1976a), (2) the problem may be tentatively considered on finite time horizon and then the terminal time is shifted to infinity (Goh 1969–70), or (3) an average cost function may be minimized (Vincent et al. 1977).

For example, when a fish population of density N is harvested at a rate u, the logistic model of the exploited population is

(5) $dN/dt = rN(K - N)/K - u$

where r and K are positive constants. To maximize the average yield from the fishery during the period $[0, T]$, T unconstrained, minimize

$$J = -\frac{1}{T} \int_0^T u dt.$$

The steady-state solution, with T unbounded, p denoting the costate and an asterisk denoting the optimal solution, is $N^* = K/2$, $p^* = 1$, $u^* = rK/4$ (Goh 1980a).

For a finite time horizon, the optimal control u, $0 \leq u(t) \leq u_{max}$ for the objective

$$\max J = \int_0^T u(t) dt$$

given (5) and $N(T) > 0$ is as follows (Goh 1980a): If $u_{max} > rK/4$, then the controls can switch among $u(t) = u_{max}$, $u(t) = 0$, or the singular control $u(t) = rK/4$, depending on time and the initial population density. If $u_{max} < rK/4$, then the optimal policy can lead to stable or unstable population density, depending on the initial conditions. When u is replaced with EN in (5), where E denotes the effort, then the optimal policy results in global equilibrium (Cliff and Vincent 1973). Thus, for a population which behaves according to the logistic model, regulation of the fisheries by effort, as opposed to quota, would result in a more stable fishery.

Optimal size limit for the Beverton and Holt (1957) model was derived by Goh (1980a). The solution depends primarily on the fish growth function and natural mortality. This is an important case, for: (1) regulating optimal size could be accomplished by mesh size regulation and (2) the approach is applicable to populations with highly variable recruitment.

Discrete Models

Formulating optimal control problems in discrete time has several advantages: many populations reproduce at discrete time intervals, and some even have nonoverlapping generations; population manipulations are usually seasonal, and can be represented by discrete events; many natural populations incorporate time lags in their dynamics, which present difficulties in continuous time optimization problems; algorithms to solve optimal control problems are discrete; mathematical programming and discrete time optimal control problems are similar (Canon et al. 1970; Tabak and Kuo 1971); singular control problems pose little difficulty in the discrete case; and abnormality (the case where there are too many constraints) can be dealt with by telescoping two or more time units (Goh 1980a).

Disadvantages of discrete time models are the theory on finite region of attraction and global stability is limited (Kalman and Bertram 1960; Diamond 1976; LaSalle 1976; Goh 1977; Fisher and Goh 1977), it is difficult to construct Liapunov functions for such models, and models with differential equations are usually more revealing and less complex for populations with overlapping generations (Nisbet and Gurney 1982). The relationships between delay differential equations and difference equations were explored by Blythe et al. (1982).

A general class of discrete time optimal control problems is the model

(6) $N(t + 1) = N(t)F[N(t)] - u(t + 1)$

where $N(t)$ denotes the post-harvest population density with discrete and nonoverlapping generations, $u(t)$ denotes the number harvested at time t, the duration of harvesting is brief and

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occurs before spawning, F is some recruitment function (e.g. Ricker 1954), and $t = 0, 1, 2, ..., T - 1$. To maximize the total yield during the period $[1, T]$, and for steady state, we need to solve the equation

$$1 = d[N(t)F(N(t))]/dN(t)$$

for N^* and apply the solution to (6). This in turn will result in optimal u^* which is also the maximum sustainable yield (MSY). The optimal control of this problem was derived by Goh (1980a), who also showed that when the harvest policy is constant quota, the MSY is unstable; when the policy is constant fraction, the MSY is locally stable.

Another important and general case of optimal control problem arises when it takes several years for an individual to reach sexual maturity (e.g. whales). The difference equation with time delays is (Clark 1976b) then

$$N(t + 1) = [1 - E(t + 1)][(sN(t) + F(N(t - 1))]$$

where $E(t + 1)$ is the fraction of the population which is harvested impulsively just before reproduction takes place, s is the fraction of adults that survive during the interval $[t, t + 1]$ in the absence of harvesting and $F(N(t - 1))$ is the recruitment to the adult population at time $t + 1$ which is due to the reproducing population at times $t - 1$. Clark (1976b) and Goh (1980a) derived the steady-state optimal solution (which maximizes yield) for this problem.

An interesting case arises when the *finite* mortality due to natural causes and due to harvesting interact (the so-called compensatory mortality). This case is important in applications, for often it is impossible to empirically establish the instantaneous rates whereas determining the finite rates of mortality is feasible (Anderson and Burnham 1975). In that case, the harvest may increase, but not without bound. Furthermore, the allowed harvest is more sensitive to changes in the amount of compensation than to changes in the finite mortality (Cohen 1986).

Multispecies Models

Current Models

Optimal control of more than two-species ecosystems poses a major difficulty, and many of the results of optimal control theory apply to two species only. Goh (1980a) proved that for two competing species with the Lotka–Voltera model, local stability implies global stability. For more than two competing species this result is not necessarily true. For any finite number of species, the Lotka–Voltera model of mutualism is globally stable if it is locally stable (Goh 1979). In a way similar to the graphical analysis of two-species interactions (MacArthur 1963), Goh (1980a) demonstrated that the nonlinear model

$$\begin{align} dN_1/dt &= N_1 F_1(N_1, N_2) \\ dN_2/dt &= N_2 F_2(N_1, N_2) \end{align} \tag{7}$$

is globally stable if (1) there is a positive equilibrium, (2) both species are self-regulating at all densities, and (3) the combined intraspecific interaction is stronger than the interspecific interactions. This is a general result, for not only is the nonlinear model (7) implicit, but the nature of interspecific interactions (e.g. predator–prey, competition, mutualism) is not specified. The system (7) remains globally stable under constant-effort harvesting policy.

For the general discrete nonlinear system model

$$N_i(t + 1) = G_i(N_1, N_2, ..., N_m)$$

where $i = 1, 2, ..., m$, Goh (1980a) derived a Liapunov function and the set of sufficient conditions for global stability.

For systems with more than two species, the optimal harvesting theory is not as well developed as for two species. Because of the added complexity, many authors (e.g. Goh 1980a; Vincent 1980) discuss only simplified mathematical models of multispecies communities. For example, a model which was analyzed extensively by Clark (1976a) includes economic as well as biological considerations, and thus renders the analysis of management options more realistic. Let

$$dN_i/dt = G_i(N) - u_i, i = 1, 2, ..., m$$

for the planning period $[0, T]$. Also, let $N_i(T) \geq e_i$, $i = 1, 2, ..., m$, where e_i is a positive constant, which is chosen such that the community remains viable after time T. Furthermore, the harvest rates are bounded from above such that

$$b_i \geq u_i(t) \geq 0, i = 1, 2, ..., m$$

where b_i is constant ($i = 1, 2, ..., m$). The problem is to choose the functions $u_i(t)$ which will drive the system from the initial state $N_i(0)$ so as to maximize the present value integral

$$J = \int_0^T e^{-\delta t} \left[\sum_{i=1}^m (v_i - c_i/N_i)u_i \right] dt$$

where v_i is the price for fish of the ith species, $c_i u_i/N_i$ is the cost of harvesting the ith species at the rate of u_i, and δ is the discount rate. Thus, we are trying to maximize the discounted net revenue (Clark 1976a; Silver and Smith 1977). The analysis of single-species models, which was not confirmed for multispecies models, suggests three stages of harvesting: (1) bring the community to a desired level as soon as possible (by allowing maximal or minimal harvest); (2) keep the community at the specified constant level until just before the end of the planning period; and (3) bring the community to the terminal state, which is specified in the problem.

Extensions to Existing Models

Little is known about the optimal fishery policy of age–size-specific models. The importance of age structure in ecological models was reviewed by Oster (1978) and Hassell (1978). Recently, Hastings and Wollkind (1982) proposed a modelling technique which allows determination of the magnitude of the effect of age structure on stability. Some authors advocate inclusion of information regarding individuals into models. For example, Botsford (1980) demonstrated that a narrow, peaked influence of older animals on recruitment over age is less stable than a broad, flat influence. Thus, the earlier conjecture that fishing stabilizes populations is not supported in all cases. This is so because age- or size-selective fishing removes animals of older ages, which narrows the influence over age of older animals on recruitment and can make the population unstable. Another interesting result is provided by the discrete time and age model of the Ricker stock–recruitment relationship. Levin and Goodyear (1980) showed that as mortality rate of older individuals is increased, it first increases and then decreases population stability, and even fishing that is not age or size selective can make a population less stable.

The traditional way of dealing with optimal harvest policy of age- or size-specific models has been restricted largely to the Leslie matrix model. Since the model is linear, harvesting is permitted only when eigenvalues are greater than 1, and optimal fishing dictates harvesting only towards the end of the planning

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period. Thus, some authors (e.g. Beddington and Taylor 1973; Rorres and Fair 1975; Rorres 1976; Mendelssohn 1976) believe that these models are of limited value.

A more realistic application of the Leslie matrix model includes stochastic fluctuations in fish populations. Numerical studies of the Leslie matrix which include stochastic fluctuations in one or more age-specific vital rates were conducted by Allen and Basasibwaki (1974), Jensen (1975), Vaughan (1977), Boyce (1977, 1979), DeAngelis et al. (1977), Deriso (1980), Christensen et al. (1982), Slade and Levenson (1982), and Ginzburg et al. (1983). More general analytical approaches of these models were studied by Cohen (1977a, 1977b, 1979a, 1979b, 1979c, 1980), Lange (1979), Lange and Hargrove (1980), Lange and Holmes (1981), and Tuljapurkar and Orzack (1980). Cohen et al. (1983) computed both the point and interval estimates of the growth rate of the average population size of the striped bass (*Morone saxatilis*). Sykes (1969) and Pollard (1966, 1973) analyzed stochastic versions of the Leslie matrix and concluded that considering the transition matrices as random variables provided a satisfactory model for estimating variances of population numbers.

It seems that when individual age–size-specific considerations are included in traditional harvesting models (e.g. logistic), the optimal harvest policy is different. For example, Botsford (1980) hypothesized that when multiple age classes with density-dependent growth and recruitment rates are included in the logistic growth model, the optimal harvesting might be pulse fishing rather than constant fishing. Similar conjecture was advanced by Clark (1976a) for models which include constant-recruitment, multiple age class. Similarly, in simulation experiments, Hannesson (1975) concluded that pulse fishing is better than stationary fishing when fishing costs are not zero. Walters (1969) obtained (numerically) the MSY dictated by models which include individual growth and stock–recruitment relationships. For the case of no fishing selectivity, he concluded that pulse fishing was optimal. When fishing selectivity was included in the model, constant harvesting policy was optimal. A similar model, with no gear selectivity, dictates pulse fishing as the optimal harvesting policy (Pope 1973).

Thus, the differences in the results of optimal harvesting policies between population models which do and do not include age- or size-specific considerations at the individual level indicate that more detailed models should be analyzed. On the other hand, inclusion of individual characteristics in multispecies models results in excessively complex models, which are difficult to deal with even with simulations. Furthermore, including age structure in single-species models usually changes the quantitative aspect of the models, but seldom affects their dynamic behavior (Nisbet and Gurney 1982). Blythe et al. (1982) argued that much of the burden of analyzing models which include age structure can be overcome by using delay-differential equations where the time lag accounts for the maturation period.

Another aspect of age-specific models is the assumption of stable age distribution (Fisher 1930; Thompson and Bell 1934; Cole 1954; Beverton and Holt 1957). The implications of relaxing this assumption have not been studied extensively (Stearns 1976), and as Sinclair et al. (1983) reported, relaxing the assumption of stable age distribution for population models of different fish species has different impacts on population production, depending on the different growth rate at different ages of various species. Thus, deviations from stable age distributions for Atlantic mackerel (*Scomber scrombus*) would have a greater impact on population production than would a similar deviation for Atlantic cod (*Gadus morhua*) (Sinclair et al. 1983).

The simplifying assumption that individuals spawn once, and at a common age, which is central to many stock–recruitment models, may result in oversight (Levin 1980). This is especially true when reproduction is spread over several age classes, such as in the striped bass. The properties of models which include multiple-age spawning were investigated, among others, by Walters (1969), Allen and Basasibwaki (1974), and Levin (1980). Generally, with the inclusion of age-specific parameters, the behavior of even the simplest fisheries models becomes more complicated, and fishing might or might not stabilize the population.

Goh (1980b) argued that for species with high fecundity and large fluctuations in recruitment, deterministic stock–recruitment models should be abandoned, and the return from using realistic stochastic models does not justify the modelling effort. Furthermore, the concept of MSY is not valid, and the best policy is to provide a set of guidelines whose objective is to prevent the collapse of the fisheries. For optimal policy of maximum biomass, these guidelines dictate optimal size limit. This approach admits that there are no long-term dynamics of the fish population. On the other hand, for species with low fecundity (e.g. whales), and when the population is large, one may use deterministic population models, and the tools of optimal control theory may be applied to derive optimal harvesting policy. This is so because the relationships between fecundity and the parent stock are well defined.

Much of both control of and inputs to ecosystems are periodic. Therefore, the topic of linear periodic control may provide some further insights into optimal control problems. This is particularly true, since the solution of the linear control problem

$$dx/dt = A(t)x + u(t),$$

where both the matrix $A(t)$ and the control vector $u(t)$ are periodic, does not in general exhibit periodic behavior of $x(t)$. Emanuel and Mulholland (1976) applied linear periodic control and derived an optimal fertilizing schedule for a sport fishing pond which should result in increased productivity.

Stability

One objective of fisheries management may be to produce a stable and reliable resource, in which case stability analysis becomes important. The general model to be considered is

(8) $dN_i/dt = N_i F_i(N_1, N_2, \ldots, N_m)$

where $F_i(N)$ are continuous functions in the positive orthant. Stability may be divided into local and global, and the distinction between them is important.

Local Stability

An ecosystem model is locally stable if every trajectory of the model which begins in the neighborhood of a particular equilibrium point remains in it for all values of time t and converges to that equilibrium point as $t \rightarrow \infty$.

When model parameters are known, local stability may be studied by linearizing (8) and applying eigenvalue analysis (May 1974). When the ecosystem model is not large (e.g. $m < 5$), and when the parameters of F in (8) are not known, the Routh–Hurwitz stability criterion may be used to establish

conditions for local stability. Another criterion which may be used to establish necessary and sufficient conditions for local stability is that of Willems (1970).

Using linear or linearized models has several advantages: the theory of linear systems is well developed, analytical solutions exist in many cases, and the optimal feedback control law for stochastic and deterministic models is the same for the general linear regulator problem (Fleming and Rishel 1975). Linear models are not totally useless, especially when the ecosystem is managed in the neighborhood of some well-defined operating point. Some authors (Nisbet and Gurney 1982) claim that examination of local stability by linearizing model equations provides much insight into the global stability of nonlinear models.

Global Stability

An ecosystem model is globally stable if every trajectory of the state variables which begins in the positive orthant remains in it for all values of time t and converges to a positive equilibrium as $t \to \infty$. Most fisheries models are nonlinear, and global stability analysis is often necessary. Global stability may be examined with the use of Liapunov functions (Liapunov 1966; Barbashin 1970; LaSalle 1976). Goh (1980a) proposed the use of two-sided energy principle in conjunction with the direct method of Liapunov. Two-sided energy principle is needed because unlike physical systems, viable populations must absorb energy at low densities and dissipate energy at high densities. Goh (1980a) derived the finite region of stability for model (8) and showed that global stability does not exist for a single species with model (8) and constant quota harvesting.

Specifically, a Liapunov function of the single-species model

$$(9) \quad dN/dt = NF(N)$$

with a positive equilibrium N^* is

$$V(N) = N - N^* - N^* \ln (N/N^*).$$

Model (9) is globally stable if $N^* > N > 0$ implies $F(N) > 0$ and if $N > N^*$ implies $F(N) < 0$ (Goh 1980a).

A multispecies system of the form

$$(10) \quad dN_i/dt = N_iF_i(N_1, N_2, ..., N_m)$$

is globally stable if (1) the equilibrium N_i^* $(i = 1, 2, ..., m)$ is in the positive orthant and (2) the interspecific interactions are weak relative to the self-regulating intraspecific interactions. For a rigorous proof, see Goh (1980a, p. 192).

As opposed to constant effort, constant quota harvesting usually results in unstable population size (Goh 1969–70; Beddington and May 1977). This is especially true when the harvesting technology is very efficient. For example, consider the single-species population exploitation model

$$(11) \quad dN/dt = NF(N) - EN$$

where E is a measure of the amount of effort applied in harvesting the popultion. If $F(N)$ is strictly monotonic decreasing as N increases, and if N has positive equilibria for both the exploited and unexploited population, then the population has global equilibria in both cases (Goh 1980a).

The above result is rather general and applies to many single-species models (e.g. Gilpin and Ayala 1973; Schoener 1973). If the population sustains an Allee effect (where a threshold population size below which the population cannot sustain itself exists; Pianka 1972), then the population model with and without harvesting may be qualitatively different.

Goh (1980a) extended model (11) to the case when both handling time of the harvested resource and competition among harvesters are considered. He then derived the conditions for stability of a general class of single-species harvesting models for $F(N)$ as in (11). Based on the results of stability analysis, it seems that regulation on the basis of effort rather than quota should be implemented wherever possible. However, as opposed to catch quotas, which are easier to monitor and apply, fishing effort is notoriously difficult to measure and quantify (Butterworth and Newman 1980).

The difficulties with analyzing global stability of ecosystems by the Liapunov or Liapunov-like method are as follows: (1) Although the literature on the construction of Liapunov functions is extensive (Schultz 1965; Hahn 1967; Gurel and Lapidus 1968, 1969; Willems 1970; Gilpin 1974; Gatto and Rinaldi 1977; Goh 1977; Hsu 1978; Goh 1980a), constructing a Liapunov function is not a trivial task, and there is no guaranteed method of finding a Liapunov function for general nonlinear systems. Hsu (1978) and Goh (1980a) have established Liapunov functions for a number of population models, and Ingwerson (1961) and Zubov (1964) proposed methods of establishing Liapunov functions for some classes of nonlinear models. (2) Since the conditions for global stability are sufficient, one has to assume that equilibrium exists before applying these methods. (3) An infinite time interval is used when a finite time interval is more useful in practice. (4) Because of the way Liapunov functions are defined, the system could be stable according to the definition, but not from a practical point of view. Nisbet and Gurney (1982) argued that the usefulness of Liapunov method for establishing global stability in ecological systems is limited.

The concept of stability is of limited value, for it establishes global stability relative to realistic perturbations from initial conditions. Most ecosystems are subject to continuous disturbance, and the concept of vulnerability is thus more useful.

Vulnerability

The concept of nonvulnerability, which describes the system ability to withstand unpredictable, large, and continual disturbances, is of much practical importance (LaSalle and Lefschetz 1961; Lashiher and Storey 1972; Goh 1975, 1976; Holling 1973; Harrison 1979; Vincent and Anderson 1979; Vincent and Skowronski 1980). This concept, which is closely related to the ideas of reachability and controllability in control systems theory (e.g. Lee and Markus 1967), was developed by Goh (1975, 1976) and Grantham and Vincent (1975).

Consider an ecosystem model during the time interval $[0, T]$. Define $S(0)$ as a set of desirable states and $Z(T)$ the set of undesirable states. Let $u_i(t)$ $(i = 1, 2, ..., n)$ be a class of continual disturbances where $u_L \leqslant u_i \leqslant u_M$ and where u_i is piecewise continuous.

The system

$$dN_i/dt = N_iF_i(N_1, N_2, ..., N_m; u_1, u_2, ..., u_n)$$

is vulnerable during $[0, T]$ if there exists an admissible set of functions $u_1(t), u_2(t), ..., u_n(t)$ which could drive the system from $S(0)$ to $Z(T)$. Otherwise the system is nonvulnerable (Goh 1980a). Vincent and Anderson (1979) have modified the above definition and analyzed vulnerability in a more qualitative way. Accordingly, they define system A to be more vulnerable than system B if any species in system A can be driven more closely to extinction than any species in system B under the disturbing function.

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Vulnerability can be analyzed with the help of Liapunov-like functions, where sufficient conditions for nonvulnerability can be examined for $[0, T]$ and $[0, \infty]$. One difficulty with this method is the numerical establishment of global maximum of a function of many variables. Another approach to the study of nonvulnerability is to set up the model ecosystem as an optimal control problem and to specify the worst possible combination of the control variables (=disturbances). The analysis in this case is very conservative.

Using the technique of Liapunov-like functions, Goh (1980a) derived the necessary conditions for nonvulnerability of a species whose population behaves according to the logistic model and who is subjected to predation by a very efficient self-regulating predator. As in the continuous case, Goh (1980a) derived the set of sufficient conditions for the existence of nonvulnerability of the system

$$N_i(t + 1) = F_i(N_1, N_2, \ldots, N_m; u_1, u_2, \ldots, u_n)$$

during the interval $[0, T]$ and $[0, \infty]$.

Using a predator–prey model with known continuous disturbance and with particular parameter values, Fisher and Goh (1980) proved that when optimal harvesting of both species is added to the system, it becomes less vulnerable in the sense that species populations are less likely to become too low; e.g. the species populations will not drop to a level below 15% of their equilibrium. Similar results were obtained for the Lotka–Voltera competition model with particular parameter values and with harvesting of only one species; i.e. the system becomes less vulnerable. The generality of these results remains to be seen.

Using the simple predator–prey model with harvesting for the baleen whale – krill system (May et al. 1979), Vincent (1980) introduced the concept of the Nash solution. For each level of sustained harvest, there is an equilibrium solution. The Nash solution is that where the sustained yield level from the system cannot be increased by increasing the effort of one harvester without affecting the harvest by other harvesters. The whale–krill model is stable under effort harvesting, and none of the species will be driven to extinction using Nash limits on the harvesting efforts. The difficulties with this approach are (1) it is assumed that none of the species is endangered at the Nash equilibrium point, (2) the prey population can be driven to a level lower than the Nash equilibrium, and thus become endangered, and (3) unless one considers a system whose major dynamics are truly dominated by two species only, there is a need to include more components in the system.

The relationships between vulnerability and return time (to equilibrium) were investigated by Vincent and Anderson (1979). It follows that when trophic levels are added to model ecosystems, the return time increases, but vulnerability may decrease. The vulnerability analysis is also useful in management under uncertainty, and optimal controller which drives the system under uncertain disturbance back to stable equilibrium was derived (Vincent 1987).

Prospects and Problems

This section lists some of the current problems and possible extensions of modelling fisheries systems.

Modelling with distributed parameter systems holds much promise. This is true because (1) modelling age and size class distributions reveals unexpected population dynamics (e.g. Botsford 1980; Levin 1980), (2) for many fish species, density distribution has strong temporal and spatial components, and (3) recently there has been much interest in biomass spectrum. Partial differential equations for some classes of age-structured populations were derived by Ahlgren (1981), Nisbet and Gurney (1982), and others. Optimal control theory of distributed parameter systems is treated in Sage (1968), Butkowskiy (1969), and Lions (1971). I am unaware of applications of distributed control systems to fisheries management.

One of the most difficult problems is to ascertain that models truly represent essential dynamics of systems. For example, vulnerability analysis with the concept of Nash equilibrium (Vincent 1980) assumes that the predator–prey model of the baleen whale – krill system (May et al. 1979) is correct. This then relates to the problem of local and global identifiability of models (Walter 1982); i.e. to what extent is a model unique in describing the relationships between inputs and outputs? Is it possible to propose other models that would give the same outputs from the same inputs? The identifiability problem is especially acute when model forecasts are used as guidelines for management decisions, when parameter estimation is crucial, and when models are used as aids for experimental design. Little attention is given to model identification in the ecological literature. This important topic is well treated by Bekey (1970), Banks (1980), Walter (1982), and others, who derived necessary conditions for local and global identifiability of state space models.

The difficulty of numerical solutions of dynamic optimal models is well recognized (Bekey 1970; Goh 1980a). Thus, it is recommended to use various algorithms with as many initial conditions as possible in solving optimal control problems (e.g. Fletcher 1975). The cost of such procedures can become prohibitive very quickly.

How can we justify ignoring certain forces within the ecosystem and claim that their consequences are negligible? It seems that often, biological mechanisms are not incorporated into mathematical models simply because they result in models which are too complicated. For example, Botsford (1980) and Sinclair et al. (1983) have demonstrated the importance of including age or size structure in fisheries models whereas Nisbet and Gurney (1982) discounted the importance of age structure in single-species population models. This problem is further compounded by the fact that when age structure is incorporated into mathematical models, they become quickly untractable, unless some questionable simplifying assumptions are adopted (e.g. see reviews by Hassell 1978; Oster 1978).

Most of the difficulties in modelling arise while building models, rather than during their analysis. For these kind of problems, little formalism exists (but see Ziegler 1976) and biological as well as mathematical sophistication is essential. Unfortunately, most scientists are competent at either one but not both subjects.

The existing fishery models all fall short of complete realistic description of population dynamics (Botsford 1980), and much effort should be invested in interpreting the biological meaning of model parameters. A lucid example was provided by Iwasa and Roughgarden (1984), who were able to interpret the biological significance of the costate variables in an optimal control problem of allocating growth to shoot/root versus reproductive tissue in plants.

Environmental conditions play an important role in determining year-class strength, and stock size may play a secondary role only (Sissenwine 1977; Van Winkle et al. 1979; Left and Kohler 1976; Nelson et al. 1976; Swartzman et al. 1983). Therefore,

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future models will have to include more environmental driving variables directly. These might enable us to account for some of the tremendous variability in recruitment. Thus, coordination of environmental and fisheries biology research should be encouraged (Butterworth and Newman 1980). In that respect, studies such as those of Swartzman et al. (1983), where age structure and ambient temperature were incorporated into a population model of the Pacific whiting (*Merluccius productus*), or Pauly (1980), who studied the relationship between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks, should be welcomed.

Incorporating economic considerations in biological models will result not only in more realistic models, but also in management objectives which might be achievable. For example, Botsford et al. (1983) demonstrated that harvest rate responds (with a lag) to fluctuations in the population of the Dungeness crab (*Cancer magister*) off the coast of California and that this lagged response is a potential cause of the population cycles. Thus, it seems that understanding the link between fluctuations in effort and fluctuations in fish populations may result in management policies which may be realistically achievable. For example, if delayed response in effort (due to market and other characteristics) contributes to population fluctuations, we may seek policies which will reduce the lag period.

Most of the modelling efforts in fisheries have concentrated on models which include biological mechanisms. Purely statistical approaches are limited (e.g. Mendelssohn 1980; Saila et al. 1980; Roff 1983), but still hold promise (e.g. Cohen et al. 1987), at least in terms of their ability to forecast (e.g. Cohen and Stone 1987). It seems that until the many problems in the mechanistic models are solved, and since policy decisions are undertaken continuously, there is room for more pragmatic models such as time series analysis (Box and Jenkins 1976).

One of the most difficult problems is to communicate the results of modelling efforts to the user (e.g. fisheries managers). This is particularly important, for many of the models in fisheries can be judged solely by their ability to help in managing the resource. A lucid review of one success story, where a model was devised, communicated, and successfully implemented, is given in Hilborn et al. (1984). Perhaps modellers need to develop a model of how models can be communicated, applied, and tested. Adaptive management (Walters 1986) is particularly useful in this respect.

It seems that the concept of MSY is not as useful as might appear from the number of publications that are dedicated to analyzing it. Furthermore, the distinction between strategic and tactic models (Nisbet and Gurney 1982) should be recognized as a continuum; both have a place in management applications. All of the applications reviewed herein are based on analytical models. They are, in most cases, limited to analysis of general models, rather than solutions of specific management problems. Other aspects of control theory, such as dynamic programming (Bellman and Kalaba 1965), are more useful for specific problems. Finally, game theory (e.g. Friedman 1971; Vincent and Gayeck 1982; Vincent and Brown 1984) will probably prove useful in future research of harvest theory and perhaps applications.

Acknowledgments

References

AHLGREN, U. 1981. Age distribution and age-class equations for simple population-growth prey–predator models. Ecol. Model. 12: 135–149.

ALLEN, R. L., AND P. BASASIBWAKI. 1974. Properties of age structure models for fish populations. J. Fish. Res. Board Can. 31: 1119–1125.

ANDERSON, D. R., AND K. P. BURNHAM. 1975. Population ecology of the mallard. VI. The effect of exploitation on survival. U.S. Fish Wildl. Ser. Res. Publ. 128: 78 p.

ATHANS, M., AND P. L. FALB. 1966. Optimal control: an introduction to the theory and its applications. McGraw-Hill, New York, NY. 550 p.

BANKS, H. T. 1980. Computational difficulties and optimization of control systems. Lect. Notes Biomath. 40: 79–94.

BARBASHIN, E. A. 1970. Introduction to the theory of stability. Wolters-Noordhoff, Groningen, The Netherlands. 223 p.

BEDDINGTON, J. R., AND R. M. MAY. 1977. Harvesting natural populations in a randomly fluctuating environment. Science (Wash., DC) 197: 463–465.

BEDDINGTON, J. R., AND D. B. TAYLOR. 1973. Optimum age specific harvesting of a population. Biometrics 19: 801–809.

BECKEY, G. A. 1970. System identification — an introduction and survey. Simulation 10: 151–166.

BELLMAN, R. 1957. Dynamic programming. Princeton University Press, Princeton, NJ. 342 p.

BELLMAN, R. E., AND R. E. KALABA. 1965. Dynamic programming and modern control theory. Elsevier, New York, NY. 365 p.

BEVERTON, R. J. H., AND S. J. HOLT. 1957. On the dynamics of exploited fish populations. U.K. Minist. Agric. Fish. Fish. Invest. (Ser. 2) 19: 533 p.

BLISS, G. A. 1946. Lectures on the calculus of variations. University of Chicago Press, Chicago, IL. 296 p.

BLYTHE, S. P., R. M. NISBET, AND W. S. C. GURNEY. 1982. Instability and complex dynamic behavior in population models with long time delays. Theor. Popul. Biol. 22: 147–176.

BOTSFORD, L. W. 1980. More realistic fishery models: cycles collapse and optimal policy. Lect. Notes Biomath. 40: 6–20.

BOTSFORD, L. W., R. D. METHOT JR., AND W. E. JOHNSTON. 1983. Effort dynamics of the northern California Dungeness crab (*Cancer magister*) fishery. Can. J. Fish. Aquat. Sci. 40: 337–346.

BOX, G. E. P., AND G. M. JENKINS. 1976. Time series analysis forecasting and control. Holden-Day, San Francisco, CA. 575 p.

BOYCE, M. S. 1977. Population growth with stochastic fluctuations in the life table. Theor. Popul. Biol. 12: 366–373.

1979. Population projections with fluctuating fertility and survivorship schedules. Proc. Summer Comp. Sim. Con. Toronto 10: 385–388.

BUTKOWSKIY, A. G. 1969. Distributed control systems. Elsevier, New York, NY. 446 p.

BUTTERWORTH, D. S., AND G. G. NEWMAN. 1980. The applications of modelling to southern African fisheries management. Lect. Notes Biomath. 33: 305–355.

CANON, M. D., C. D. CULLUM, AND E. POLAK. 1970. Theory of optimal control and mathematical programming. McGraw-Hill, New York, NY. 285 p.

CHRISTENSEN, S. W., C. P. GOODYEAR, AND B. L. KIRK. 1982. An analysis of the validity of the utilities' stock–recruitment curve-fitting exercise and "prior estimation of beta" technique. The impact of entrainment and impingement on fish populations in the Hudson River Estuary. Vol. III. ORNL/NUREG/TM-385/V3 (NUREG/CR-2220/V3). Oak Ridge National Laboratory, Oak Ridge, TN.

CLARK, C. W. 1973. The economics of over-exploitation. Science (Wash., DC) 181: 630–634.

1976a. Mathematical bioeconomics: the optimal management of renewable resources. Wiley, New York, NY. 352 p.

1976b. Delayed-recruitment model of population dynamics with an application to baleen whale population. J. Math. Biol. 3: 381–392.

CLARK, C. W., F. H. CLARKE, AND G. R. MUNRO. 1979. The optimal exploitation of renewable resource stocks: problems of irreversible investment. Econometrica 47: 25–47.

CLIFF, E. M., AND T. L. VINCENT. 1973. An optimal policy for a fish harvest. J. Opt. Theor. Appl. 12: 485–496.

COHEN, J. E. 1977a. Ergodicity of age structure in populations with Markovian vital rates. II. General states. Adv. Appl. Prob. 9: 18–37.

1977b. Ergodicity of age structure in populations with Markovian vital rates. III. Finite-state moments and growth rates: illustration. Adv. App. Prob. 9: 462–475.

1979a. Long-run growth rates of discrete multiplicative processes in Markovian environments. J. Math. Anal. Appl. 69: 243–251.

1979b. Ergodic theorems in demography. Bull. Am. Math. Soc. N.S. 1: 275–295.

1979c. Comparative statics and stochastic dynamics of age structured populations. Theor. Popul. Biol. 16: 159–171.

1980. Convexity properties of products of random non-negative matrices. Proc. Natl. Acad. Sci. USA 77: 3749–3752.

COHEN, J. E., S. W. CHRISTENSEN, AND C. P. GOODYEAR. 1983. A stochastic age structured population model of striped bass (Morone saxatilis) in the Potomac River. Can. J. Fish. Aquat. Sci. 40: 2170–2183.

COHEN, Y. 1986. On the relationships between natural and harvest mortalities of the mallard (Anas platyrhynchos). Nat. Res. Model. 1: 105–110.

COHEN, Y., AND J. N. STONE. 1987. Multivariate time series analysis of the Canadian fisheries system in Lake Superior. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 171–181.

COHEN, Y., J. N. STONE, AND T. L. VINCENT. 1987. Vulnerability, stability, and coherence of the fish community in Lake Superior. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 404–410.

COLE, L. C. 1954. The population consequences of life history phenomena. Q. Rev. Biol. 29: 103–137.

DEANGELIS, D. L., S. W. CHRISTENSEN, AND A. G. CLARK. 1977. Responses of a fish population model to young-of-the-year mortality. J. Fish. Res. Board Can. 34: 2124–2132.

DERISO, R. B. 1980. Harvesting strategies and parameter estimation for an age structured model. Can. J. Fish. Aquat. Sci. 37: 268–282.

DIAMOND, P. 1976. Domains of stability and resilience for biological populations obeying difference equations. J. Theor. Biol. 61: 287–306.

EMANUEL, W. R., AND R. J. MULHOLLAND. 1976. Linear periodic control with applications to environmental systems. Int. J. Control 24: 807–820.

FISHER, R. A. 1930. The genetical theory of natural selection. Dover, New York, NY. 325 p.

FISHER, M. E., AND B. S. GOH. 1977. Stability in a class of discrete time models of interaction populations. J. Math. Biol. 4: 265–274.

1980. Nonvulnerability of two species interactions. Lect. Notes Biomath. 40: 133–150.

FLEMING, W. H., AND R. W. RISHEL. 1975. Deterministic and stochastic optimal control. J. Inst. Math. Appl. 15: 319–342.

FLETCHER, R. 1975. An ideal penalty method for constrained optimization. J. Inst. Math. Appl. 15: 319–342.

FRIEDMAN, A. 1971. Differential games. Wiley, New York, NY. 371 p.

GATTO, M., AND S. RINALDI. 1977. Stability analysis of predator–prey models via the Liapunov method. Bull. Math. Biol. 39: 339–347.

GILPIN, M. E. 1974. A liapunov function for competition in communities. J. Theor. Biol. 44: 35–48.

GILPIN, M. E., AND E. J. AYALA. 1973. Global models of growth and competition. Proc. Natl. Acad. Sci. USA 79: 3590–3593.

GINZBURG, L. R., K. JOHNSON, A. PUGLIESE, AND J. GLADDEN. 1983. Ecological risk assessment based on stochastic age-structured models of population growth. Proc. Symp. Stat. Environ. Sci. American Society for Testing and Materials, Philadelphia, PA.

GOH, B. S. 1966a. The second variation of the singular Bolza problem. SIAM J. Control 4: 309–325.

1966b. Necessary conditions for singular extremals involving multiple control variables. SIAM J. Control 4: 716–731.

1969–70. Optimal control of a fish resource. Malay. Sci. 5: 65–70.

1975. Stability, vulnerability and persistence of complex ecosystems. Ecol. Model. 1: 105–116.

1976. Nonvulnerability of ecosystems in unpredictable environments. Theor. Popul. Bio. 10: 83–95.

1977. Stability in a stock recruitment model of an exploited fishery. Math. Biosci. 33: 359–372.

1979. Stability in models of mutualism. Am. Nat. 113: 261–275.

1980a. Management and analysis of biological populations. Elsevier, Amsterdam, The Netherlands. 288 p.

1980b. Modelling and management of fish populations with high and low fecundities. Lect. Notes Biomath. 40: 54–63.

GOH, B. S., AND T. T. AGNEW. 1978. Stability in a harvested population with delayed recruitment. Math. Biosci. 42: 187–197.

GOH, B. S., G. LEITMANN, AND T. L. VINCENT. 1974. The optimal control of a prey–predator system. Math. Biosci. 19: 263–286.

GOPALSAMY, K. 1980. Optimal stabilization and harvesting in logistic population models. Ecol. Model. 11: 67–69.

GRANTHAM, W. J., AND T. L. VINCENT. 1975. A controllability minimum principle. J. Optim. Theor. Appl. 17: 93–114.

GUREL, O., AND L. LAPIDUS. 1968. Stability via Liapunov's second method. Ind. Eng. Chem. 60: 1–26.

1969. A guide to the generation of Liapunov functions. Ind. Eng. Chem. 61: 30–41.

HAHN, W. 1967. Stability of motion. Springer-Verlag, Berlin. 446 p.

HANNESSON, R. 1975. Fishery dynamics: a North Atlantic cod fishery. Can. J. Econ. 8(2): 151–173.

HARRISON, G. W. 1979. Persistent sets via Liapunov functions. Nonlinear Anal. 3: 73–80.

HASSELL, M. P. 1975. Density dependence in single-species populations. J. Anim. Ecol. 44: 283–295.

1978. The dynamics of arthropod predator–prey systems. Princeton University Press, Princeton, NJ. 237 p.

HASTINGS, A., AND D. WOLLKIND. 1982. Age structure in predator–prey systems. I. A general model and a specific example. Theor. Popul. Biol. 21: 44–56.

HILBORN, R., C. J. WALTERS, R. M. PETERMAN, AND M. J. STALEY. 1984. Models and fisheries: a case study in implementation. N. Am. J. Fish. Manage. 4: 9–14.

HOLLING, C. S. 1973. Resilience and stability of ecological systems. Annu. Rev. Ecol. Syst. 4: 1–23.

HSU, S. B. 1978. On global stability of a predator–prey system. Math. Biosci. 39: 1–10.

INGWERSON, D. R. 1961. A modified Liapunov method for non-linear stability analysis. IRE Trans. AC-6: 199–210.

IWASA, Y., AND J. ROUGHGARDEN. 1984. Shoot/root balance of plants: optimal growth of a system with many vegetative organs. Theor. Popul. Biol. 15: 78–105.

JENSEN, A. L. 1975. Computer simulation of effects on Atlantic menhaden yield of changes in growth, mortality, and reproduction. Chesapeake Sci. 16: 139–142.

KALMAN, R. E., AND J. E. BERTRAM. 1960. Control system analysis and design via the second method of Liapunov. II. Discrete time systems. ASME J. Basic Eng. 82: 371–393.

LANGE, K. 1979. On Cohen's stochastic generalization of the strong ergodic theorem of demography. J. Appl. Prob. 16: 496–504.

LANGE, K., AND J. HARGROVE. 1980. Mean and variance of population size assuming Markovian vital rates. Math. Biosci. 52: 289–301.

LANGE, K., AND W. HOLMES. 1981. Stochastic stable population growth. J. Appl. Prob. 18: 325–334.

LARSON, R. E. 1968. State increment dynamic programming. Elsevier, New York, NY. 225 p.

LASALLE, J. P. 1976. The stability of dynamical systems. Society for Industrial and Applied Mathematics, Philadelphia, PA. 76 p.

LASALLE, J. P., AND S. LEFSCHETZ. 1961. Stability by Liapunov's direct method with applications. Academic Press, New York, NY. 134 p.

LASHIHER, A. M., AND C. STOREY. 1972. Final stability with some applications. J. Inst. Math. Appl. 9: 397–410.

LEE, E. B., AND L. MARKUS. 1967. Foundations of optimal control theory. Wiley, New York, NY. 576 p.

LEFT, P. F., AND A. C. KOHLER. 1976. Recruitment: a problem of multispecies interaction and environmental perturbations, with special reference to Gulf of St. Lawrence Atlantic herring (Clupea harengus harengus). J. Fish. Res. Board Can. 33: 1353–1371.

LEVIN, S. A. 1980. Age-structure and stability in multiple age spawning population. Lect. Notes Biomath. 40: 21–45.

LEVIN, S. A., AND C. P. GOODYEAR. 1980. Analysis of an age-structured fishery model. J. Math. Biol. 9: 245–275.

LIAPUNOV, A. M. 1966. Stability of motion. Academic Press, New York, NY. 203 p.

LIONS, J. L. 1971. Optimal control of systems governed by partial differential equations. Springer-Verlag, New York, NY. 396 p.

LUENBERGER, D. G. 1969. Optimization by vector space methods. Wiley, New York, NY. 250 p.

MACARTHUR, R. H. 1963. Fluctuations of animal populations and a measure of community stability. Ecology 36: 533–536.

MAY, R. M. 1974. Stability and complexity in model ecosystems. Princeton University Press, Princeton, NJ. 265 p.

MAY, R. M., J. R. BEDDINGTON, C. W. CLARK, S. J. HOLT, AND R. M. LAWS. 1979. Management of multispecies fisheries. Science (Wash., DC), 205: 267–277.

MENDELSSOHN, R. 1976. Optimization problems associated with a Leslie matrix. Am. Nat. 110: 339–349.

1980. Using Box–Jenkins models to forecast fishery dynamics: identification, estimation and checking. Fish. Bull. 78: 887–896.

MORAN, P. A. P. 1950. Some remarks on animal dynamics. Biometrics 6: 251–258.

NELSON, W. R., M. G. INGRAM, AND W. P. SCHAAF. 1976. Larval transport and year class strength of Atlantic menhaden, Brevoortia tryananis. Fish. Bull. 75: 23–41.

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NISBET, R. M., AND W. S. C. GURNEY. 1982. Modelling fluctuating populations. Wiley, New York, NY. 379 p.

OSTER, G. 1978. The dynamics of nonlinear models with age structure, p. 411–476. *In* S. A. Levin [ed.] Studies in mathematical biology, Part III. Mathematical Association of America, Washington, DC.

PAULY, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. Int. Explor. Mer 39: 175–192.

PIANKA, E. R. 1972. *R* and *k*-selection or *b* and *d* selection? Am. Nat. 106: 581–588.

POLLARD, J. H. 1966. On the use of the direct matrix product in analysing certain stochastic population models. Biometrica 53: 397–415.

1973. Mathematical models for the growth of human populations. Cambridge University Press, London. 373 p.

PONTRYAGIN, L. S., V. G. BOLTYANSKII, R. V. GAMKRELIDZE, AND E. F. MISHCHENKO. 1962. The mathematical theory of optimal processes. Wiley, New York, NY. 360 p.

POPE, J. G. 1973. An investigation into the effects of variable rates of the exploitation of fishery resources. *In* M. S. Bartlett and R. W. Hiorns [ed.] The mathematical theory of dynamics of biological populations. Academic Press, New York, NY.

RICKER, W. E. 1954. Stock and recruitment. J. Fish. Res. Board Can. 11: 559–623.

ROFF, D. A. 1983. Analysis of catch/effort data: a comparison of three methods. Can. J. Fish. Aquat. Sci. 40: 1496–1506.

RORRES, C. 1976. Optimal sustainable yields of a renewable resource. Biometrics 32: 945–948.

RORRES, C., AND W. FAIR. 1975. Optimal harvesting policy for an age-specific population. Math. Biosci. 24: 31–47.

SAGE, A. P. 1968. Optimum systems control. Prentice-Hall, Englewood Cliffs, NJ. 373 p.

SAILA, S. B., M. WIGBOUT, AND R. J. LERMIT. 1980. Comparison of some time series models for the analysis of fisheries data. J. Cons. Int. Explor. Mer 39: 44–52.

SCHOENER, T. W. 1973. Population growth regulated by intraspecific competition for energy or time: some simple representations. Theor. Popul. Biol. 4: 56–84.

SCHULTZ, D. G. 1965. The generation of Liapunov functions, p. 1–64. *In* C. T. Leondes [ed.] Advances in control systems. Vol. 2. Academic Press, New York, NY.

SILVER, W., AND W. R. SMITH. 1977. Optimal exploitation of a multi-species community. Math. Biosci. 33: 121–134.

SINCLAIR, M., R. O'BOYLE, AND T. D. ILES. 1983. Consideration of the stable age distribution assumption in "analytical" yield models. Can. J. Fish. Aquat. Sci. 40: 95–101.

SISSENWINE, M. P. 1977. A compartmentalized simulation model of the southern New England yellowtail flounder, *Limanda ferruginea*, fishery. Fish. Bull. 75: 465–482.

SLADE, N. A., AND H. LEVENSON. 1982. Estimating population growth rates from stochastic Leslie matrix. Theor. Popul. Biol. 22: 229–308.

STEARNS, S. C. 1976. Life-history tactics: a review of the ideas. Q. Rev. Biol. 51: 3–47.

SWARTZMAN, G. L., W. M. GETZ, R. C. FRANCIS, R. T. HAAR, AND K. ROSE.

1983. A management analysis of the Pacific whiting (*Merluccius productus*) fishery using an age-structured stochastic recruitment model. Can. J. Fish. Aquat. Sci. 40: 524–539.

SYKES, Z. M. 1969. Some stochastic versions of the matrix model for population dynamics. J. Am. Stat. Assoc. 64: 111–130.

TABAK, D., AND B. C. KUO. 1971. Optimal control by mathematical programming. Prentice-Hall, Englewood Cliffs, NJ. 240 p.

THOMPSON, W. F., AND F. H. BELL. 1934. Biological statistics of the Pacific halibut fishery. (2) Effect of changes in intensity upon total yield and yield per unit of gear. Rep. Int. Fish. (Pacific Halibut) Comm. 8: 1–49.

TULJAPURKAR, S., AND S. ORZACK. 1980. Population dynamics in variable environments. I. Long-run growth rates and extinction. Theor. Popul. Biol. 18: 314–342.

VAN WINKLE, W., B. L. KIRK, AND B. W. RUST. 1979. Periodicities in Atlantic coast striped bass (*Morone sexatilis*) commercial fisheries data. J. Fish. Res. Board Can. 36: 54–62.

VAUGHAN, D. S. 1977. Confidence intervals on mortality rates based on the Leslie matrix, p. 128–150. *In* W. Van Winkle [ed.] Assessing the effects of power-plant-induced mortality on fish populations. Pergamon Press, New York, NY.

VINCENT, T. L. 1980. Vulnerability of a pre-predator model. Lect. Notes Biomath. 40: 112–132.

1987. Modeling and management in the presence of uncertain inputs. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 267–274.

VINCENT, T. L., AND L. R. ANDERSON. 1979. Return time and vulnerability for a food chain model. Theor. Popul. Biol. 15: 217–231.

VINCENT, T. L., AND J. S. BROWN. 1984. Stability in an evolutionary game. Theor. Popul. Biol. 26: 408–427.

VINCENT, T. L., AND J. E. GAYECK. 1982. A game theoretic analysis for renewable resource management. Ecol. Model. 14: 213–227.

VINCENT, T. L., C. S. LEE, AND B. S. GOH. 1977. Control targets for the management of biological systems. Ecol. Model. 3: 285–300.

VINCENT, T. L., AND J. M. SKOWRONSKI [ED.] 1980. Renewable resource management. Lect. Notes Biomath. 40.

WALTER, E. 1982. Identifiability of state space models. Lect. Notes Biomath. 46.

WALTERS, C. J. 1969. A generalized computer simulation model for fish population studies. Trans. Am. Fish. Soc. 98: 505–512.

1975. Optimal harvest strategies for salmon in relation to environmental variability and uncertain production parameters. J. Fish. Res. Board Can. 32: 1777–1784.

1986. Adaptive management of renewable resources. MacMillan, New York, NY.

WALTERS, C. J., AND R. HILBORN. 1976. Adaptive control of fishing systems. J. Fish. Res. Board Can. 33: 145–159.

WICKWIRE, K. 1977. Mathematical models for the control of pests and infectious diseases; a survey. Theor. Popul. Biol. 1: 182–238.

WILLEMS, J. L. 1970. Stability theory of dynamical systems. Nelson, London, 201 p.

ZIEGLER, B. P. 1976. Theory of modelling and simulation. Wiley, New York, NY. 435 p.

ZUBOV, V. I. 1964. Methods of A. M. Liapunov and their application. Noordhoff, The Netherlands. 251 p.

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