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THRESHOLD MANAGEMENT STRATEGIES FOR EXPLOITED FISH POPULATIONS

By:

Jie Zheng

A thesis presented to the Faculty
of the University of Alaska Fairbanks
in partial fulfillment of the requirements
for the degree of

Doctor of Philosophy

1994

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A

THESIS

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Juneau, Alaska

May 1994

ABSTRACT

Under a threshold management strategy, harvesting occurs at a constant rate but ceases when a population drops below a threshold. The threshold approach seeks to enhance long-term yield of a population and to maintain population renewability. I evaluated threshold management strategies for selected herring and pollock stocks in Alaska.

First, I examined stock-recruitment data from 19 major herring stocks worldwide to provide the basis for evaluating threshold management strategies. Seventy-three percent of these stocks exhibited statistically significant density-dependence. Most stocks have compensatory, dome-shaped stock-recruitment curves.

Then, I simulated threshold management strategies for eastern Bering Sea (EBS) pollock and herring and Prince William Sound (PWS) herring using a single-species model. I further examined seven alternative threshold estimation methods. Cohort analysis, catch-at-age analysis, and catch and population sampling yielded estimates of population parameters. The objective function was a weighted function of increased average yield and decreased standard deviation of yield over a planning horizon. Compared to a non-threshold approach, threshold management strategies increase the long-term average yields, stabilize population abundances, shorten rebuilding times, and increase management flexibility.

For a maximum yield criterion and Ricker stock-recruitment models, optimal fishing mortalities are slightly above fishing mortalities at maximum sustained yield (MSY), and optimal threshold levels range from 40% to 60% of pristine biomass for EBS pollock, from 40% to 50% for EBS herring and from 30% to 60% for PWS herring. With fishing mortality at MSY and the criterion of equal trade-off between yield and its variation, optimal thresholds range from 20% to 30% of pristine biomass for pollock. With the status quo exploitation rate of 20%, optimal thresholds range from

10% to 25% of pristine biomass for EBS herring, and from 5% to 25% for PWS herring.

Of the threshold estimation methods evaluated, default percentage of pristine biomass usually performs best. Loss of yield due to errors in threshold estimation is small, generally under 10%. About 15 to 20 years of data are required to obtain a reliable estimate of thresholds. With single-species dynamics, the form of the stock-recruitment curve, exploitation rate and management objective are the most important factors affecting optimal thresholds.

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ACKNOWLEDGEMENTS

I thank the members of my supervisory committee, Drs. R. Fagen, T.J. Quinn II, G.H. Kruse, J.S. Collie, J.P. Lambert, J.F. Fox, and D.L. Musgrave, for their guidance, advice, support and helpful criticisms. Dr. R. Hollister served on the supervisory committee for one year during Dr. J.P. Lambert's sabbatical leave. In particular I thank Drs. R. Fagen, T.J. Quinn II, and G.H. Kruse, and Mr. F.C. Funk, for providing me the opportunity to conduct this research and for their effort toward this study. Chapters three to five of this dissertation are based on the information from the three papers in which they are co-authors. Cohort analysis and catch-age analysis on eastern Bering Sea pollock and Prince William Sound herring for these three papers were conducted by Dr. T.J. Quinn II and Mr. F.C. Funk, respectively. The co-authors of these three papers supervised the research, contributed ideas and helped revise the papers.

I am deeply grateful to V. Wespestad of the NOAA Alaska Fisheries Science Center (NMFS) for providing population parameters and catch-age data of walleye pollock and herring in the eastern Bering Sea and his results of cohort analyses for this study. Herring stock-recruitment data were provided by J.F. Schweigert of Pacific Biological Station for British Columbia stocks, by F.C. Funk and D. Carlile of the Alaska Department of Fish and Game for Southeast Alaska stocks, and by J.P. Wheeler of Canadian Department of Fisheries and Oceans for Newfoundland stocks. Many staff in Alaska Department of Fish and Game contributed ancillary data or provided advice on data analysis.

This study was financially supported by the Alaska Department of Fish and Game and the Alaska Sea Grant College Program supported by NOAA, Office of Sea Grant and Extramural Programs under grant NA86AA-D-SG041 project M/80-01, PR87-06PD to Drs. T.J. Quinn II and R. Fagen. Partial financial support was also provided by the University of Alaska Fairbanks, Office of the Graduate School, through a Graduate Resource Fellowship.

I owe the most to my wife, Ling Li, for her emotional support and patience on too many long evenings and weekends. I thank our first child, Pauline Zheng, for providing me joy whenever I was tired of books and computer, and our second child whose birth we are anxiously awaiting and who kept reminding me of finishing my dissertation before he comes to this world. We extend our sincere appreciation to Mrs. F. Arnold who deeply understands the challenges and opportunities facing Chinese students in the U.S. and is always standing by to offer help to new arrivals and old.

Chapter One

INTRODUCTION

Two kinds of overfishing could occur for an exploited fish population: growth and recruitment overfishing (Cushing 1977). Growth overfishing results from harvesting fish so young that they do not have a chance to grow to optimal sizes. Recruitment overfishing occurs when the spawning stock is reduced to a low level due to heavy fishing so that recruitment is seriously affected. Growth overfishing has been recognized since early this century (Cushing 1977) and is easily detected and avoided. Recruitment overfishing may be disastrous and cause a population to lose its renewability, but it is difficult to detect. After several important fisheries, like the Hokkaido-Sakhalin herring (*Clupea pallasi*), the Norwegian herring (*Clupea harengus*), the Japanese sardine (*Sardinops melanosticta*), the Californian sardine (*Sardinops sagax*) and the Peruvian anchovy (*Engraulis ringens*), collapsed during periods when fishing was high (Cushing 1971), recruitment overfishing has increasingly been an important concern for fisheries management.

Currently there is much interest in the development of harvest strategies to ensure that fisheries resources are optimally utilized and that fish populations are not overfished. As one example, the North Pacific Fishery Management Council, responsible for management of U.S. groundfish resources in the northeastern Pacific Ocean, adopted definitions of acceptable biological catch (ABC) and other management terms in 1988 that attempt to provide for both conservation and optimal utilization of the resources. The ABC was defined as "an acceptable level of harvest which recognizes the status and dynamics of the stock, environmental conditions, and ecological factors" and "must equal zero when the stock is at or below its threshold". The ABC definition contains the concept of a threshold, a low population level below which there would be concern about the ability of the population to increase and fishing would be prohibited.

To promote the wise use and conservation of fish resources, the Secretary of Commerce of the United States Government promulgated the national standard definitions of fisheries management terms in 1989. These standards (section 602 of the Federal Guidelines for Fishery Management Plans) list threshold as a "minimum level of spawning biomass" and provide the option (but not requirement) of specifying threshold levels for each managed fish population. Each fishery management plan for species managed by the United States was required to be amended in 1990 to define overfishing for each stock on the basis of a maximum fishing mortality and/or a threshold population level.

A threshold management strategy seeks to prevent recruitment overfishing and to optimally utilize fisheries resources. The threshold management strategy is defined in this study such that harvest occurs at a constant exploitation rate but ceases when a population drops below a threshold. For a given population, the most difficult tasks are to judge whether a threshold approach can outperform a non-threshold approach in terms of management objectives, and how to choose an optimal threshold level.

The threshold concept has evolved from the fixed escapement policy used frequently in Pacific salmon management (Reed 1979; Getz and Haight 1989), with the difference being that not all surplus fish are harvested under a threshold approach. The threshold approach prohibits fishing to protect the population and to promote population rebuilding when the population drops to a very low level. Optimal harvesting policies have been derived or simulated for age-structured population models with both deterministic and stochastic recruitment (Rorres and Fair 1975; Reed 1980; Deriso 1985, 1987; Horwood 1987; Getz and Haight 1989), but a threshold level has rarely been explicitly embedded.

The threshold concept is relatively new to fishery management. Beddington and Cooke (1983) used 20% of the average unexploited spawning biomass as a threshold (or targeted spawning biomass level) to study the potential yield of fish stocks with constant harvest rate and constant catch policies. Ruppert et al. (1984, 1985) introduced a general harvesting policy that includes a threshold level to explore optimal harvesting strategies of the Atlantic menhaden (*Brevoortia tyrannus*) fishery. This general harvesting policy was used by Hightower and Lenarz (1989) to examine optimal harvesting policies for the widow rockfish (*Sebastes entomelas*) fishery. Hilborn (1985) applied a simple general harvesting policy with a threshold policy as a special case to compare harvest policies for mixed-stock fisheries. The above studies either used threshold as a constraint to compare other harvesting policies, or compared the threshold policy with other policies in terms of average yield or logarithm of yield. In their study of alternative harvest strategies for Pacific herring (*Clupea pallasi*) in the Strait of Georgia, British Columbia, Hall et al. (1988) compared the threshold policy with constant harvest rate and constant escapement policies using three criteria: average catch, catch variance and risk. None of these studies estimated optimal thresholds.

Most work with thresholds has occurred in conservation biology, and especially in the study of endangered species (Mode and Jacobson 1987a; Soule 1987). The common goal in conservation biology is to maintain the health and diversity of natural biological systems---ecosystems, communities, habitats, as well as species. A population threshold, also called minimum viable population size, is usually determined for a species, especially endangered species, so that appropriate landscapes and habitats can be preserved to avoid population from extinction (Shaffer 1983; Lande 1987; Mode and Jacobson 1987b). Extinction is a probabilistic phenomenon, and time frame and security levels are important factors to determine a population threshold level (Shaffer 1987; Mode and Jacobson 1987b; Wissel and Stocker 1991). Shaffer (1981) reviewed the five methods of determining population thresholds: experiments, biogeographic patterns, theoretical models, simulation models and genetic considerations, and concluded that the most promising approaches are biogeographic patterns and computer simulations.

The important distinction between the concepts of population thresholds in fisheries management and conservation biology stems from the different management objectives. While a threshold serves as a conservative measure for both commercial fish and endangered wildlife populations, it is also used as a tool to enhance long-term yields for exploited fish populations. The concept of economic extinction furnishes a bridge between these two disciplines. Economic extinction, defined as long-term depression of a population below the minimum level necessary to sustain an economically feasible harvest, may be the first step on the road to biological extinction. Thresholds for exploited fish populations are generally chosen to meet economic objectives and to prevent economic extinction, while thresholds for endangered wildlife populations emphasize the prevention of biological extinction.

Threshold management policies have been applied to some fish populations worldwide, especially pelagic species. A threshold level of 15 to 25% of either pristine spawning biomass or average observed spawning biomass has been established for Pacific herring in British Columbia, Canada, and Washington and Alaska, USA (Trumble and Humphreys 1985). Although a threshold level was not specified, the North Sea herring fishery was closed in the late 1970's and the early 1980's when the population dropped down to a low level (Jakobsson 1985). Spawning biomasses of 50,000 tonnes and 600,000 tonnes have been used as thresholds for the northern anchovy (*Engraulis morax*) off the coast of California and Atlantic mackerel (*Scomber scombrus*) in the northeast Atlantic, respectively (J. Collie, personal communications). Many crab stocks in Alaska have been managed with a threshold level which is used to enhance the renewability and productivity of the stocks (Schmidt and Pengilly 1990). For groundfish in western Canada, one of the possible management options is to stop fishing when a stock falls below a certain level, although currently there are no stocks so managed (Fargo and Tyler 1989).

Compared with a constant harvest rate approach, the threshold approach has an advantage in terms of stable population size. The population is less prone to lose its renewability and more likely to move toward improved long-term yield levels. Threshold management strategies were shown to be effective for stock conservation and increasing total yield for chub mackerel (*Scomber japonicus*) in Japan under a fluctuating environment (Matsuda et al. 1992). The threshold approach is especially beneficial to rebuilding a depressed population. A simulation study of an overexploited Pacific ocean perch (*Sebastes alutus*) stock in British Columbia demonstrated that rebuilding would be enhanced when fishing mortality was reduced or curtailed (Archibald et al. 1983).

The disadvantages of the threshold approach are that the potential to prohibit harvesting in some years may increase short-term harvest variation and adversely affect the short-term economic well-being of users. All threshold management strategies to date have been based on a single-species approach. It may be difficult to extend threshold approaches to multi-species fisheries because of lack of detailed knowledge on species interactions. When several species are harvested in the same fishery, bycatch problems may be further complicated by threshold management policies. If the assessment and management of a fishery primarily depends on commercial catch data, the required data will not be available when the threshold takes effect.

In contrast to the threshold approach, a non-threshold approach, such as constant harvest rate, has the advantage of easy implementation. Traditionally, constant harvest rate is one of the most common management strategies (Getz and Haight 1989) and several fishing mortality reference levels, such as [1]$F_{0.1}$, F_{max}, F_{rep}, F_{MSY}, and F_{mmy}, have been very well documented and applied to a variety of populations (Alverson and Pereyra 1969; Gulland and Boerema 1973; Deriso 1987; Hightower and Grossman 1985; Sissenwine and Shepherd 1987; Clark 1991). Data requirements for estimation of fishing mortality levels are relatively flexible.

The constant harvest rate approach reduces variance in harvest, at the cost of increased variance in population levels. It is beneficial to maintain a stable harvest if alternate fisheries are not available. But some of the commonly-used fishing mortality

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[1] $F_{0.1}$ is the fishing mortality at which the slope of the yield per recruit curve as a function of fishing mortality is equal to 10% of its value at the origin. F_{max} is the fishing mortality at which the yield per recruit is maximized. F_{rep} is the fishing mortality at which the spawning biomass per recruit is reduced to the median value observed in a set of stock-recruitment data. F_{MSY} is the fishing mortality that produces the maximum sustained yield for a population. F_{mmy} is the fishing mortality that maximizes the minimum yield among all the stock-recruitment relationships considered.

rates ($F_{0.1}$, F_{max}, and F = instantaneous natural mortality) are estimated from life history parameters alone and their effects on spawners and subsequent recruitment are not taken into account. These mortality rates may potentially deplete a stock if a period of poor recruitment occurs. Even with a well-estimated fishing mortality rate, it is still questionable whether this approach can reasonably maximize the returns from exploiting the resources and provide necessary protection when the population levels are low, especially when multi-species conservation criteria are also imposed.

Successful application of threshold management policies to fish populations requires the development of methods to estimate and evaluate threshold levels on fish population abundance and yield. If the threshold level is set too low, then it will not provide sufficient protection for depleted populations to recover. If set too high, then prohibition of harvesting will deprive harvesters of justifiable harvesting opportunities.

Two species, walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea and Pacific herring in Alaska, will be the subject of my numerical study. These two species provide contrast in population dynamics of groundfish versus pelagic fish. Pollock populations tend to grow and decline rapidly and have comparatively high mortalities. The pollock population in the eastern Bering Sea is of immense commercial importance and is one of the most important components in its ecosystem (NPFMC 1991; Laevastu and Larkins 1981). Pollock is a semi-demersal species and classified as "groundfish" in commercial fisheries. Cannibalism and predation are two important biological features of pollock.

Herring is a pelagic species and is one of the most common fish species throughout the world and well known for its fluctuations in abundance. In Alaska, large-scale commercial harvest of herring started in 1920's, and now this species supports one of the most important fisheries in the state (Funk and Harris 1992). Ad hoc threshold levels have been established for different stocks of herring in Alaska. This study will evaluate these ad hoc threshold levels and suggest new optimal threshold levels consistent with current management objectives. As generic models and computer software have been developed for these two species, the methodology can be applied to other species.

In this study I examined herring stock-recruitment data around the world to illustrate the need for a threshold management strategy because understanding the recruitment dynamics of fish stocks is crucial to selecting harvest strategies. Then population parameters of eastern Bering Sea pollock and herring and Prince William Sound herring were estimated and collected. Threshold management strategies were evaluated for these three populations based on single-species models. Evaluation criteria include an objective function, risk of overharvesting and rebuilding time, as well as robustness to errors in estimation or implementation. The objective function is the trade-off between increased average yield and decreased variation in yield over a planning horizon of 20 to 50 years. The risk is defined here as the probability that a population drops below a defined threshold level. The rebuilding time is total number of years for a population to take to rebuild from an initial biomass to the biomass producing MSY. I will address the following questions: 1) What data and techniques are required to estimate threshold levels? 2) Given a harvesting rate and an objective function, which threshold approach performs best? 3) What are the important factors affecting optimal threshold levels? 4) How much can we gain by using a threshold approach, compared with a non-threshold approach such as a constant harvest rate strategy?

The dissertation is presented in seven chapters. Chapter two discusses the relation between spawners and recruitment of herring worldwide and herring recruitment patterns. It was generally believed in the past that herring recruitment is regulated by environmental factors and that density-dependent effects on herring recruitment are weak or non-existent. This chapter is intended to test for density-dependent effects on herring recruitment statistically and to examine at what spatial scale environmental forces influence herring year-class strengths. Chapter three deals with threshold management policies for the eastern Bering Sea pollock population. Threshold management strategies for Alaska herring are evaluated in chapter four. Two of the largest herring stocks in Alaska, eastern Bering Sea and Prince William Sound stocks, are examined. Chapter five compares and evaluates seven different threshold estimation methods through computer simulations. Chapter six summarizes the results of sensitivity analyses of optimal thresholds with different population parameters, environmental noises, harvest levels and management objectives. The results in previous chapters are integrated to identify key factors influencing optimal threshold levels. The final chapter summarizes the conclusions for this study and discusses the limitations.

Chapter Two

HERRING STOCK-RECRUITMENT RELATIONSHIPS AND RECRUITMENT PATTERNS IN THE NORTH ATLANTIC AND NORTHEAST PACIFIC OCEANS

SUMMARY

Recruits are the youngest age group in a fishery. Understanding the recruitment dynamics of marine fish stocks is crucial in selecting harvest strategies. Revealing the recruitment patterns is the first step to understanding the recruitment dynamics. In this study, stock-recruitment data of 19 major herring stocks from the north Atlantic and northeast Pacific Oceans were examined for density-dependent effects on recruitment and for recruitment patterns over spatial scales. Two parametric and one nonparametric tests indicate that the survival rates from eggs to recruits from about 73% of stocks are related to spawning biomass, with high spawning biomass resulting in low survival rates. Close to half the stocks show that year-class strengths are associated with spawning biomass. Most stocks have compensatory, dome-shaped stock-recruitment curves. Positive correlations are generally found among the geographically close neighbor stocks. The recruitment patterns suggest each environmental process may play an important role in recruitment dynamics of herring only within a certain spatial scale.

INTRODUCTION

Understanding the recruitment dynamics of a stock is essential for optimal uses of the resource and maintenance of its renewability. The recruitment rate is one of the most important determinants of the capacity of a stock to sustain exploitation (Getz et al. 1987; Quinn et al. 1990). Recruitment dynamics also determine harvest management strategies applied to the stock. If recruitment is not related to the corresponding spawning stock, yield per recruit or economic return per recruit is a natural choice for the harvest management strategy (Beverton and Holt 1957). Otherwise, other management strategies should be used (Getz and Haight 1989). Thus, the problem of recruitment dynamics lies at the heart of fisheries management.

Stock-recruitment relationships describe the density-dependent variation of recruitment. The commonly used stock-recruitment models were developed by Ricker (1954) and Beverton and Holt (1957). Both models were derived from assumptions of density-dependent predation and/or food limitation. The Ricker model requires mortality to be dependent on spawning stock abundance, whereas the Beverton-Holt model has mortality dependent on pre-recruit densities over a sequence of stages from eggs to recruits. The Ricker curve is dome-shaped, with maximum recruitment occurring at an intermediate level of spawning stock. The Beverton-Holt curve is asymptotic. Deriso (1980) described a general stock-recruitment model which includes the Ricker, Beverton-Holt, constant recruitment and Schaefer models (Schaefer 1957) as special cases. Cushing (1971) derived another common stock-recruitment model, relating density-dependence to fecundity. Fish with low fecundities are expected to have a near-linear relationship of recruitment with spawners, whereas the Ricker dome-shaped curves would be characteristic of fish with high fecundities. Shepherd (1982) developed a general model which can mimic the Ricker and Cushing curves and includes the Beverton-Holt model as a special case. A Markov probability transition matrix model is also commonly used to describe stock-recruitment relationships (Getz and Swartzman 1981; Swartzman et al. 1983; Overholtz et al. 1986).

Stock-recruitment models have been fitted to a variety of data sets on marine fishes (Cushing 1973; Cushing and Harris 1973; Csirke 1980; Jakobsson 1980; Buck and Hay 1984; Garrod and Jones 1974; Huang and Walters 1983). The models often explain only a small proportion of the recruitment variation. The apparent lack of stock-recruitment relationships in many fish stocks can be attributed to measurement errors in both stock and recruitment data (Walters and Ludwig 1981), stochasticity of actual recruitment, or the actual lack of relationship between recruitment and spawning stock over the observed range of data.

The difficulty of using spawning stock to explain variation of recruitment has led to innumerable correlation studies in which recruitment indices are correlated with one or more environmental variables (Davydov 1989; Donnelly 1983; Chebanov 1989; Koslow et al. 1987; Lasker 1978; Shepherd et al. 1984; Wespestad 1991; Quinn and Niebauer *in press*; Zebdi and Collie *in press*). Based on an assumption that recruitment success is primarily determined by physical factors, these correlation studies aim at understanding of recruitment variation and prediction of recruitment. Although some environmental factors may have a plausible causal mechanism to affect spawning success and pre-recruit survival, and in some cases regressions are highly significant, few of these predictions of recruitment have stood the test of time. As pointed out by Walters and Collie (1988): "It is entirely too easy to find spurious correlations".

Another approach is to examine the recruitment patterns of different fish stocks within or between regions to determine whether recruitment is regulated through large-scale environmental forcing or biological interactions (Koslow 1984). If recruitment is controlled primarily by large-scale environmental forcing, positive correlation should be evident among recruitment for the same species over broad spatial scales (Koslow 1984). On the other hand, if recruitment is predominantly regulated through biological interactions, stock-recruitment relationships should be evident. Koslow (1984) examined recruitment patterns in northwest Atlantic fish stocks and concluded that large-scale physical forcing primarily regulates recruitment. Hollowed et al. (1987) expanded Koslow's study to northeast Pacific stocks and found that recruitment success is strongly influenced by environmental conditions. Pepin (1990) studied biological correlations of recruitment variability in North Sea stocks and suggested that the dominant association is between fluctuations in recruitment and plankton abundance.

In this paper, I examined stock-recruitment data of 19 herring stocks from the north Atlantic and northeast Pacific Oceans. First, density-dependent effects and stock-recruitment relationships were examined, aiming at testing the hypothesis that recruitment of herring is independent of its spawning stock size and at examining the shape of stock-recruitment curves. Then, recruitment patterns were studied to determine the possible role of large-scale physical forcing in herring recruitment variation.

METHODS

Data

Time series of recruitment and spawning biomass for 19 herring stocks from the north Atlantic and northeast Pacific Oceans (*Clupea harengus* and *Clupea pallasi*) were collected from various sources (Table 2.1 and Figure 2.1). These time series were derived either by virtual population analysis (VPA) tuned by auxiliary information or catch-at-age analysis with auxiliary information. Recruitment is defined as ages 1, 2 or 3, depending on stock, and was identified by brood year termed "year-class". The estimates of stock and recruitment in the most recent years are highly influenced by fishing mortality and auxiliary information in the terminal year. To reduce this uncertainty, I discarded the data after year-class 1986, i.e., at least the data in the most recent three years were discarded. The abundances at age 0 for Norwegian spring spawning stock were multiplied by 0.51 (the survival rate from the lightest fishing year-class 1950 during 1950-1969) to get recruitment at age 3 from 1950 to 1969 because juvenile herring of this stock suffered high fishing mortality during this period (Dragesund et al. 1980) and the recruitment data after 1969 are available only at age 3 (Anonymous 1993). In this study, I accepted the stock definitions in the data sources because the stock-recruitment data are available only for the defined stocks.

Stock-recruitment Relationships

Four approaches were used to test the two null hypotheses: 1) per capita recruitment is independent of spawning stock size and 2) total recruitment is independent of spawning stock size. First, Cushing (1971) proposed a simple stock-recruitment model:

$$(2.1) \qquad R = a S^{b}$$

where R is recruitment, S is spawning biomass, a is a constant and b is an index of density dependence. When b is negative and as S approaches zero, R approaches

Table 2.1. Summary of data sources for 19 herring stocks.

Stock	Notation	Year-Class	Data Source
1 North Sea	NSea	48-90	Anonymous (1992)
2 ICES District Via North	ViaN	70-89	Anonymous (1993)
3 Icelandic summer spawners	IceSum	48-89	Anonymous (1993)
4 Icelandic spring spawners	IceSpr	48-72	Jakobsson (1980)
5 Norwegian spring spawners	Norwe	50-69	Dragesund et al.(1980)
		70-89	Anonymous (1993)
6 Gulf of Maine	Maine	66-90	NEFC (1992)
7 Newfoundland WBNDB	WBNDB	64-82	Wheeler et al. (1985)
8 Newfoundland CBTB	BBTB	64-82	Wheeler et al. (1985)
9 Newfoundland CBSS	CBSS	64-82	Wheeler et al. (1985)
10 Eastern Bering Sea	EBS	56-89	Zheng et al.(*in press* a)
11 Prince William Sound, AK	PWS	69-89	Funk & Zheng (1992a)
12 Sitka Sound, AK	Sitka	68-89	D. Carlile, ADF&G
13 Seymour Canal, AK	Seymour	73-89	D. Carlile, ADF&G
14 Kah Shakes, AK	KahS	73-89	D. Carlile, ADF&G
15 Prince Rupert, BC	BCPR	48-89	Schweigert et al.(1993)
16 Queen Charlotte Is., BC	BCQCI	48-89	Schweigert et al.(1993)
17 Central Coast, BC	BCCC	48-89	Schweigert et al.(1993)
18 West Vancouver Is.,BC	BCWVI	48-89	Schweigert et al.(1993)
19 Strait of Georgia, BC	BCSG	48-89	Schweigert et al.(1993)

Abbreviations:
WBNDB: White Bay-Notre Dame Bay
CBTB: Bonavista Bay-Trinity Bay
CBSS: Conception Bay-Southern Shore
AK: Alaska, USA
BC: British Columbia, Canada.

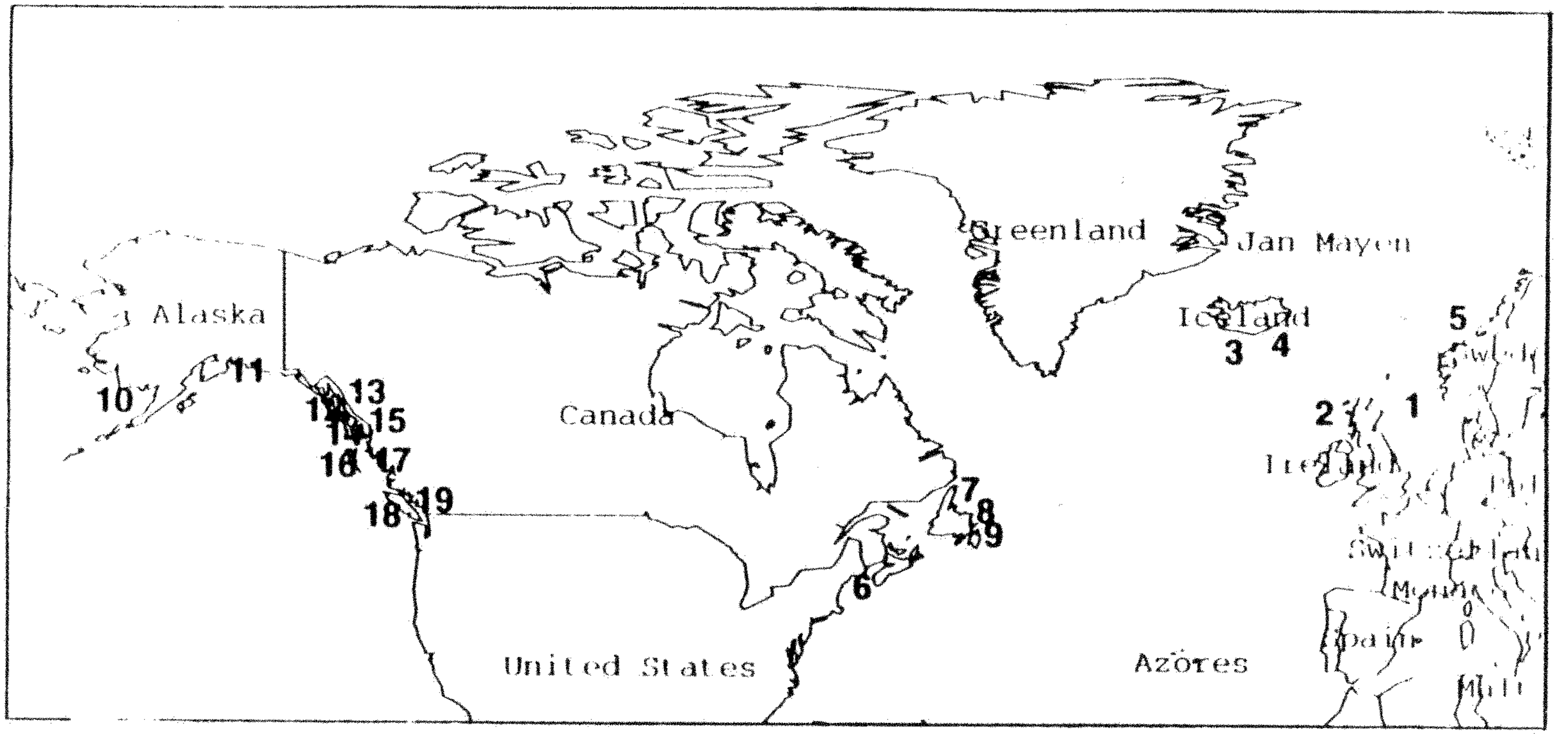

Figure 2.1. The north Atlantic and northeast Pacific Oceans with locations of 19 herring stocks. See Table 2.1 for notation of the stock number.

infinity, so the Cushing model is unrealistic for some data ranges. But the model is handy for testing recruitment density-dependence. Linearizing equation (2.1) results in:

(2.2) $\ln(R) = \ln(a) + b \ln(S)$.

Thus, testing the null hypotheses is equivalent to testing b values. Parameters a and b were estimated by an ordinary linear regression. Log transformation of recruitment reduces the influences of outliers of stock-recruitment data on parameter estimation and gives an equal weight to each data point. Parameter b measures the degree of density dependence of stock-recruitment data (Cushing 1971). If b is not significantly different from 1, then the per capita recruitment (or the survival rate from egg to recruit) is independent of egg density (null hypothesis (1)) because spawning biomass is approximately proportional to fecundity for herring (Ware 1985). If b is not significantly different from 0, then total recruitment (or year-class strength) is independent of spawning biomass (null hypothesis (2)).

Secondly, I used Ricker's stock-recruitment model to test density-dependence of recruitment. The Ricker model is

(2.3) $R = \alpha\ S \exp(-\beta\ S + v_t)$

and is linearized as

(2.4) $\ln(R/S) = \ln(\alpha) - \beta\ S + v_t$

where

$$v_t = \sigma_t + \alpha_1\ v_{t-1} + \alpha_2\ v_{t-2}$$

and t stands for time (year), α and β are parameters, and v_t is a noise term. In contrast to the common assumption of normality of v_t (Walters 1986), I assumed v_t as being autocorrelated over time as some recruitment data indicated. σ_t is normally and independently distributed with mean of 0; α_1 and α_2 are autocorrelation coefficients. An autocorrelation regression (procedure AUTOGRE, SAS Institute Inc. 1988) with a maximum likelihood method was used to estimate parameters α, β, α_1 and α_2. The advantage of autocorrelation regression is to reduce the influence of the noise term on the parameter estimates in the autocorrelation process. If β is significantly different from

0, we can reject the null hypothesis (1). In addition, autocorrelation coefficients α_1 and α_2 were tested for significance for each data set.

Thirdly, a nonparametric classification technique (Rothschild and Mullen 1985) was used to classify the stock-recruitment data. A chi-square test (for data sets with 30 or more data points) and Fisher's exact test (for data sets with less than 30 data points) were applied to test the null hypothesis (2). A 2*3 classification utilized the median recruitment, 1/3 quantile and 2/3 quantile of spawning biomass to divide stock-recruitment data into 6 categories. Quantile is the same as percentile except that quantile refers to a fraction of a data set while percentile refers to a percent of a data set. A value of 1 was assigned to a datum when recruitment was equal to or above the median; otherwise 0 was assigned.

Finally, a LOWESS (locally weighted regression scatter plot smoothing) procedure (Becker et al. 1988) was used to robustly smooth the logarithm of recruitment data against spawning biomass to reveal stock-recruitment relationships. Log transformed recruitment data reduced the influence of extreme year-classes and residuals derived from the smoothed curve approximated a normal distribution. I used 0.5 as the fraction parameter f in the LOWESS procedure (Becker et al. 1988) to achieve a relatively good fit for all data. The null hypotheses were not tested statistically, but examined visually.

Recruitment Patterns

Three forms of recruitment data transformations were used to examine recruitment patterns for herring: 1) log-transformed recruitment (Log(R)), 2) first order differences of log-transformed recruitment (Dlog(R), i.g., for a given year t, $\mathrm{Dlog}(R_t) = \log(R_{t+1}) - \log(R_t)$) , and 3) residuals from the LOWESS curves (Lowess-Res). Log transformation of recruitment minimizes the influences of extreme year-classes, normalizes the data, and emphasizes long-term, low frequency variations (Koslow 1984; Hennemuth et al. 1980). First-order differences of log-transformed recruitment filter out low frequency variations and first-order autocorrelation of recruitment, and concentrate on short-term, high frequency variations (Pepin 1990; Thompson and Page 1989). Residuals from fitted stock-recruitment curves reflect recruitment variation independent of spawning stock size.

All time series of recruitment data in each of these three forms were tested for normality by the Lilliefors test (Conover 1980, p357). The null hypothesis of normality was rejected for only 3 out of 57 data sets at a significance level of 0.05. Thus, Pearson's product-moment correlation coefficients were used to test whether recruitment data sets between any two stocks are significantly correlated.

Hierarchical cluster analyses were conducted on 15 stocks for year-classes 1973-1986 for each of these three data forms. The other 4 stocks were excluded because their data did not completely overlap this time period. The distance for clustering was obtained through 1 minus the correlation matrix and average distance was used for clustering.

Year-class strengths were summarized in terms of ratio of maximum to minimum recruits, coefficient of variation, and frequency of stronger than average year-classes. These statistics provide direct comparisons of year-class variations and skewness of recruitment distributions from different stocks.

RESULTS

Stock-recruitment Relationships

Two approaches were used to study the relationships of herring stock-recruitment: the two null hypotheses were tested statistically and then stock-recruitment data were smoothed to reveal the relationships. Table 2.2 summarizes the test statistics. The recruitment for three stocks (Prince William Sound, Sitka, and Kah Shakes) was too variable to reject the null hypothesis of $b = 0$ or $b = 1$. For the remaining 16 stocks, only two stocks (the Icelandic spring spawners and Norwegian spring spawners) have b values not significantly different from 1 at 0.05 level (Table 2.2). The b values for all other stocks were significantly less than 1, i.e., per capita recruitment decreases as the spawning stock increases and thus the stock-recruitment relationships are

Table 2.2. Summary of test statistics of density independence for herring recruitment from 19 stocks.

Stock	Cushing Model			Ricker Model							Nonpar.
	b	p(=0)	p(=1)	-β*S	pa	pn	α_1	$p_{\alpha 1}$	α_2	$p_{\alpha 2}$	p
1 NSea	0.52	.000	.000	-0.76	.000	.000	0.20	.222	0.34	.044	.007
2 ViaN	0.15	.425	.000	-0.75	.005	.001	0.00	.996	0.19	.537	.589
3 IceSum	0.52	.001	.001	-0.57	.119	.027	0.46	.011	0.02	.910	.003
4 IceSpr	1.20	.000	.097	-0.43	.433	.630	0.72	.013	0.17	.553	.001
5 Norwe	0.88	.000	.266	-0.15	.409	.310	0.14	.464	0.02	.897	.000
6 Maine	0.10	.446	.000	-0.82	.002	.000	0.19	.463	0.07	.770	.536
7 WBNDB	-1.81	.024	.002	-2.06	.117	.002	0.38	.242	0.25	.499	.004
8 BBTB	-1.79	.006	.000	-3.60	.000	.000	0.51	.103	-0.49	.157	.004
9 CBSS	-0.91	.094	.003	-1.72	.065	.009	0.73	.053	-0.23	.513	.301
10 EBS	-0.52	.089	.000	-1.89	.000	.000	0.42	.052	-0.16	.492	.047
11 PWS	0.50	.534	.540	-0.70	.369	.635	0.02	.442	-0.57	.076	.037
12 Sitka	0.49	.338	.316	-0.53	.296	.600	0.59	.057	-0.71	.028	.145
13 Seymour	-0.72	.087	.001	-1.83	.002	.000	0.17	.649	-0.41	.402	.056
14 KahS	-0.69	.375	.048	-1.77	.055	.074	-0.12	.803	-0.27	.605	.455
15 BCPR	0.09	.688	.000	-0.85	.018	.000	0.49	.011	-0.07	.707	.097
16 BCQCI	0.14	.444	.000	-0.97	.001	.000	0.31	.088	-0.05	.787	.717
17 BCCC	0.08	.654	.000	-1.13	.000	.000	0.08	.683	-0.06	.754	.264
18 BCWVI	0.10	.581	.000	-0.86	.008	.002	0.41	.032	0.07	.713	.264
19 BCSG	0.34	.046	.000	-1.02	.000	.000	0.55	.005	-0.06	.759	.013

Abbreviations:

b: value of parameter b in equation (2.1)

p(=0): p value for null hypothesis of b = 0

p(=1): p value for null hypothesis of b = 1

β*S: value of parameter β in equation (2.3) times mean spawning biomass

pa: p value for null hypothesis of β = 0 with autocorrelation regression

pn: p value for null hypothesis of β = 0 with ordinary regression

α_1: autocorrelation coefficient with a time lag of one year

$p_{\alpha 1}$: p value for null hypothesis of $\alpha_1 = 0$

α_2: autocorrelation coefficient with a time lag of two years

$p_{\alpha 1}$: p value for null hypothesis of $\alpha_2 = 0$

p: p value for chi-square test of density independence.

compensatory. Thus hypothesis (1) was rejected for 14 out of 16 stocks. The *b* values for two of the Newfoundland stocks were significantly less than zero at 0.05 level (Table 2.2), suggesting an overcompensatory stock-recruitment relationship.

Testing $b = 0$ is equivalent to testing the null hypothesis (2). The null hypothesis (2) was rejected for 6 out of the 9 Atlantic stocks and for 1 out of the 10 Pacific stocks with a significance level of 0.05. Overall, more than 50% of stocks failed to reject the null hypothesis. With a significance level of 0.1, the null hypothesis was rejected for 10 out of 19 stocks.

The nonparametric classification tests the null hypothesis (2) by a different statistical method. Results generally resemble the test of $b = 0$. For 9 and 11 out of 19 stocks, the null hypothesis was rejected at significance levels of 0.05 and 0.1, respectively. The results also suggest that herring recruitment in the northeast Pacific is less dependent on spawning biomass than recruitment to the north Atlantic stocks (Table 2.2).

An alternative index of density dependence is the product of $-\beta$ from the Ricker curve and mean spawning biomass (Cushing and Harris 1973; Winters and Wheeler 1987). The indices for all 19 stocks varied from -0.15 to -3.6 and were all negative (Table 2.2), indicating the compensatory stock-recruitment curves. Fourteen out of the 19 stocks rejected the null hypothesis (1) of $\beta = 0$ with an ordinary Ricker model at a significance level of 0.05 (Table 2.2). When autocorrelations with time lags of 1 and 2 years were included in the Ricker model, only 11 out of the 19 stocks rejected the null hypothesis (1). The autocorrelation coefficients with a time lag of 1 year were generally positive and ranged from -0.12 to 0.73, with most of them less than 0.4. Only 5 out of the 19 stocks had autocorrelation coefficient α_1 significantly different from 0 at 0.05 probability level. Autocorrelation coefficient α_2 was not significantly different from 0 in 17 out of the 19 stocks. Although not shown here, no stocks had significant autocorrelation coefficients with a time lag of more than 2 years.

The LOWESS procedure was used to smooth the stock-recruitment data. The stock-recruitment relationships are population-dependent. For the Pacific stocks, strong dome-shaped stock-recruitment curves occurred with the Seymour Canal and the Strait of Georgia stocks, and weak dome-shaped curves occurred with the eastern Bering Sea, the central coast of British Columbia and Prince Rupert stocks (Figure 2.2). The year-class strengths appeared independent of spawning biomass for the Queen Charlotte Island and the west coast of Vancouver Island stocks. No meaningful stock-recruitment relationships were found for the Prince William Sound, Sitka Sound, and Kah Shakes stocks.

Stock-recruitment relationships were better defined for the Atlantic stocks than the Pacific stocks. A curve with a shape between a Beverton-Holt curve and a Ricker curve was revealed for the North Sea, Icelandic spring spawning and Norwegian spring spawning stocks, with weak recruits associated with low spawning biomass (Figure 2.3). A dome-shaped curve was apparent for the stock in ICES district Via north. Lower and much more variable recruitments were associated with low spawning biomasses than with high spawning biomasses for the Icelandic summer spawning stock. Strong dome-shaped curves were evident for the three Newfoundland stocks, with weak recruitments associated with high spawning biomasses. No apparent stock-recruitment relationship was found for the Gulf of Maine stock.

Recruitment Patterns

Recruitment data were transformed in three ways (Log(R), Dlog(R), and Lowess-Res) and compared in Figure 2.4. Dlog(R) represented high frequency components in the recruitment data and were more variable than Log(R) and Lowess-Res data. Lowess-Res data were similar to Log(R) data for stocks in which spawning biomass explained little variation of recruitment.

Table 2.3 summarizes the p-value matrices for testing correlation between the recruitment data for different stocks. The p value gives the probability of obtaining a value of the test statistic at least as unfavorable to null hypothesis as the observed value. Correlations were much stronger among stocks in the same region than stocks in different regions. For Log(R) data, extremely strong positive correlations existed among

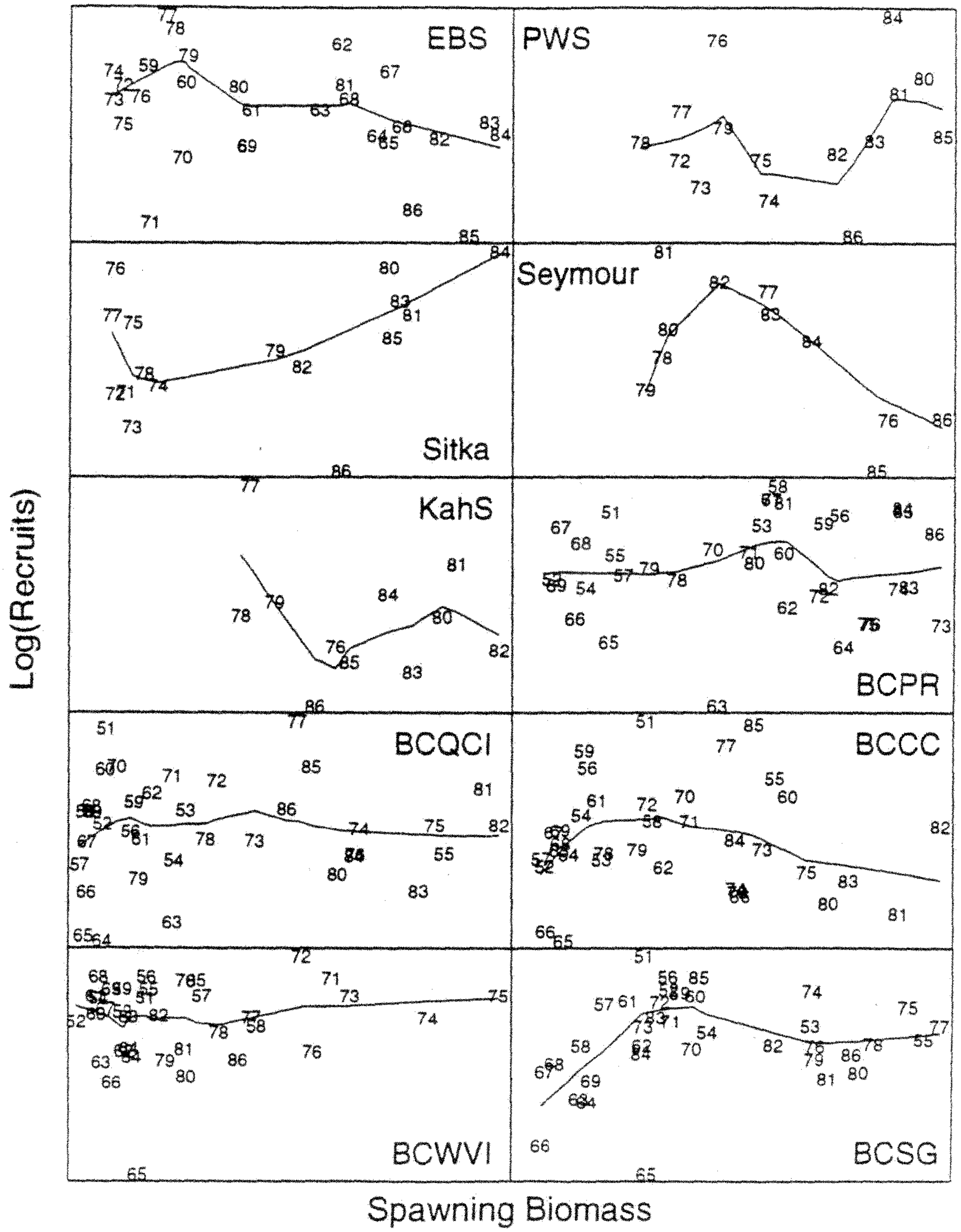

Figure 2.2. Stock-recruitment relationships for 10 herring stocks in the northeast Pacific Ocean. The numbers in the plots are brood-year and the solid lines are the LOWESS fitted curves. The data have been scaled from minimum to maximum values. See Table 2.1 for stock notations.

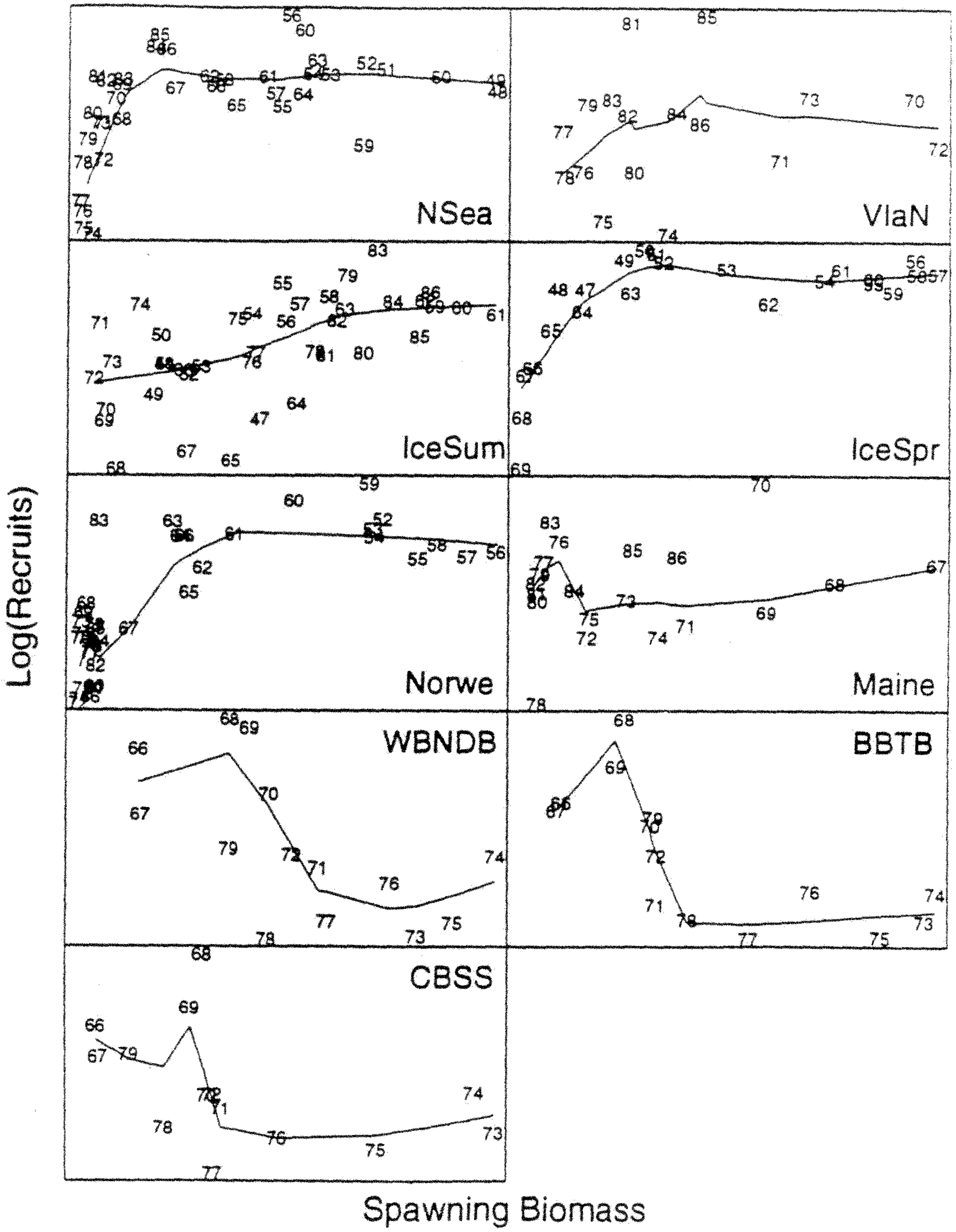

Figure 2.3. Stock-recruitment relationships for 9 herring stocks in the north Atlantic Ocean. The numbers in the plots are brood-year and the solid lines are the LOWESS fitted curves. The data have been scaled from minimum to maximum values. See Table 2.1 for stock notations.

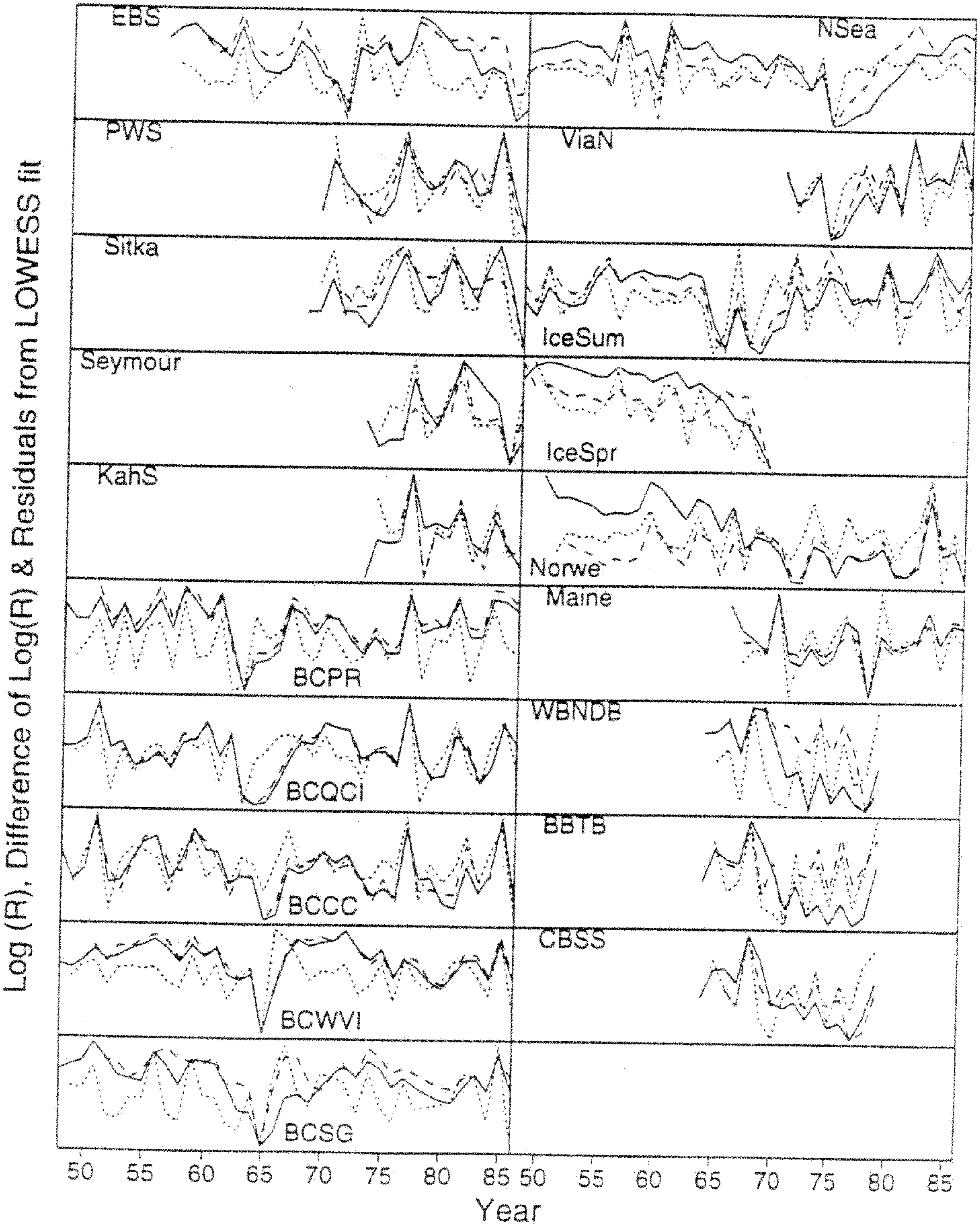

Figure 2.4. Time series data of log-transformed recruitment (solid lines), first-order difference of log-transformed recruitment (dotted lines), and residuals from the LOWESS fitted curves (dashed lines) for 19 herring stocks. See Table 2.1 for stock notations.

Table 2.3. P values for the null hypothesis that the correlation coefficient equals 0 for 19 herring stocks. Negative sign indicates a negative correlation coefficient. See notation for stock number in Table 2.1. (NA denotes the time series data are not overlapped so that no correlation can be tested).

a. Log Transformed Recruitment data

Stock	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1 NSea	.00	.73	.10	.01	.09	.00	.00	.01	-.09	.84	-.80	.46	-.45	.12	-.83	.33	-.78	-.97
2 ViaN		-.84	NA	.40	.05	.52	.18	.57	-.22	.52	.84	.35	.89	.02	.38	.19	.90	-.51
3 IceSum			.00	.37	-.87	-.01	-.00	-.02	.58	-.66	.54	-.75	-.48	.54	-.97	.43	.51	.01
4 IceSpr				.00	NA	NA	NA	NA	.06	NA	NA	NA	NA	.31	.50	.16	.84	.00
5 Norwe					.03	.01	.04	.04	.16	.92	.52	-.95	-.50	-.83	-.25	.23	.99	.36
6 Maine						.13	.21	.55	-.18	.24	.22	.97	-.80	.56	-.82	.87	-.47	-.22
7 WBNDB							.00	.00	-.11	-.88	-.52	NA	NA	-.86	-.25	-.37	-.50	-.01
8 BBTB								.00	-.39	-.92	-.45	NA	NA	.89	-.26	-.40	-.47	-.01
9 CBSS									-.37	-.31	-.16	NA	NA	.99	-.22	-.23	-.53	-.02
10 EBS										.52	.35	.13	.03	.68	.97	.93	-.94	.54
11 PWS											.00	.26	.05	.23	-.67	.89	-.17	-.24
12 Sitka												.30	.06	.50	-.30	-.84	-.10	-.66
13 Seymour													.05	.28	.85	-.71	-.35	-.03
14 KahS														.03	.13	.33	-.35	-.35
15 BCPR															.00	.00	.03	.00
16 BCQCI																.00	.00	.00
17 BCCC																	.00	.00
18 BCWVI																		.00
19 BCSG																		.00

Table 2.3 (continue)

b. First Difference of Log Transformed Recruitment data

Stock	2	3	4	5	6	7	8	9	10
1 NSea	.02	-.53	.18	.82	.72	-.22	-.45	-.38	-.34
2 ViaN		-.39	NA	.19	.04	-.82	.71	-.61	-.96
3 IceSum			-.30	.03	.71	.59	-.31	-.97	-.64
4 IceSpr				-.63	NA	NA	NA	NA	-.65
5 Norwe					.04	.16	.53	.39	-.78
6 Maine						.49	.46	-.65	-.95
7 WBNDB							.00	.00	.69
8 BBTB								.00	.45
9 CBSS									.94
10 EBS									
11 PWS									
12 Sitka									
13 Seymou									
14 KahS									
15 BCPR									
16 BCQCI									
17 BCCC									
18 BCWVI									
19 BCSG									

11	12	13	14	15	16	17	18	19
.53	-.80	.57	-.42	-.96	.63	.93	-.69	-.67
.77	.97	.80	.55	.25	.14	.13	.17	.72
-.18	-.32	-.73	.99	-.25	-.34	-.52	.85	-.93
NA	NA	NA	NA	.46	-.40	.92	-.81	.54
-.63	.80	-.38	-.44	-.01	-.07	-.84	.37	.42
.28	.16	-.90	.82	.83	.76	.52	-.82	-.99
.73	.33	NA	NA	-.77	-.84	-.42	-.64	-.60
.65	.42	NA	NA	-.60	-.47	-.28	-.28	-.28
-.49	-.62	NA	NA	-.44	-.32	-.07	-.33	-.33
.85	.74	.02	.02	.30	.22	-.63	-.61	-.81
	.00	.84	.42	.35	-.81	-.91	-.15	-.25
		-.98	.35	.43	-.90	.78	-.61	.97
			.06	.10	.22	-.93	-.64	-.15
				.00	.01	.21	-.91	.97
					.00	.01	.17	.13
						.00	.04	.01
							.00	.00
								.00
								.00

Table 2.3 (continue)

c. Residuals from LOWESS Fit Stock-Recruitment Data

Stock	2	3	4	5	6	7	8	9	10
1 NSea	.00	-.63	.67	-.90	.68	-.17	-.50	-.43	-.55
2 ViaN		-.05	NA	.25	.19	-.24	.65	-.13	.81
3 IceSum			.34	.62	-.91	-.82	-.25	-.55	-.64
4 IceSpr				-.03	NA	NA	NA	NA	.55
5 Norwe					.31	.68	.04	.25	.39
6 Maine						.11	.70	.67	-.06
7 WBNDB							-.82	.02	-.13
8 BBTB								.19	.06
9 CBSS									-.44
10 EBS									
11 PWS									
12 Sitka									
13 Seymour									
14 KahS									
15 BCPR									
16 BCQCI									
17 BCCC									
18 BCWVI									
19 BCSG									

11	12	13	14	15	16	17	18	19
-.96	-.39	.27	-.61	.28	.78	.57	-.78	-.44
-.98	-.70	.61	.27	.03	.44	.07	.64	-.11
-.30	-.70	-.80	-.54	.91	.61	.66	.10	.03
NA	NA	NA	NA	.30	-.62	-.97	-.36	.79
-.90	.49	-.30	-.46	-.69	-.25	.30	.31	.41
-.61	-.40	-.50	.66	.28	.39	.21	.46	-.47
.69	-.99	NA	NA	-.67	.33	.94	.50	-.94
.53	.33	NA	NA	.71	-.17	-.16	-.22	.46
-.60	-.66	NA	NA	-.99	-.71	-.38	.56	.49
.18	.12	.11	.28	-.78	-.37	-.47	-.33	.66
	.00	.89	.09	.80	-.77	.92	-.19	-.28
		-.86	.28	-.30	-.37	-.88	-.28	.80
			.24	.88	.74	-.19	-.14	-.01
				.27	.11	.42	-.67	-.63
					.00	.00	.01	.01
						.00	.00	.00
							.00	.00
								.00
								.00

all 5 stocks in British Columbia, among 3 stocks in Newfoundland, between the Prince William Sound and Sitka Sound stocks, between the North Sea and ICES district Via north stocks, and between the Icelandic summer spawning and Norwegian spring spawning stocks (Table 2.3a). Among significant inter-regional comparisons, stocks of North Sea and Norwegian spring spawners were positively correlated to three Newfoundland stocks which were in turn negatively associated the Icelandic summer spawning stock and the Strait of Georgia stock in British Columbia. The Kah Shakes stock in Southeast Alaska was positively and significantly correlated with all stocks from the eastern Bering Sea to Prince Rupert in the northern part of British Columbia. However, the Seymour stock in Southeast Alaska did not associate with any of these stocks other than the Kah Shakes stock.

After filtering out the low frequency signals by differencing, correlations among the Dlog(R) data were less significant than the Log(R) data. For the Dlog(R) data, the correlations were generally positive among stocks within the same region and negative among stocks in different regions (Table 2.3b). But the correlations among stocks in different regions were very weak, with most of p values larger than 0.2. With a significance level of 0.05, significant correlations occurred between the North Sea and ICES district Via north stocks, between the Icelandic summer spawning and Norwegian spring spawning stocks, between Norwegian spring spawners and the Gulf of Maine stocks, and among the three stocks in Newfoundland. Of the Pacific stocks, the eastern Bering Sea stock did not associate with its neighbor stock of Prince William Sound, but with the Seymour and Kah Shakes stocks in Southeast Alaska. The Prince William Sound and Sitka Sound stocks were strongly correlated with each other, but not with other stocks. The stocks in the central and southern British Columbia were strongly associated with each other, but the Prince Rupert stock was correlated only with its neighbor Queen Charlotte Island and central coast stocks in British Columbia and the Kah Shakes stock in the Southeast Alaska.

After removing the influences of spawning biomass, the correlations among stocks with the same region decreased (Table 2.3c). For the LOWESS-Res data, the strong positive correlations still held between the North Sea and ICES district Via north stocks, between the White Bay-Notre Dame Bay and Conception Bay-Southern Shore stocks in Newfoundland, between the Prince William Sound and Sitka Sound stocks. and among the stocks in British Columbia.

Three large clusters were found with the Log(R) data: an Atlantic group (Icelandic summer spawners, Norwegian spring spawners, the Gulf of Maine, North Sea and ICES district Via north), a central and southern British Columbia group (West Vancouver Island, Strait of Georgia, Queen Charlotte Island and central coast of British Columbia), and a northern Pacific group (eastern Bering Sea, Seymour Canal, Prince William Sound, Sitka Sound, Kah Shakes and Prince Rupert) (Figure 2.5). These three groups did not relate to each other. Within each group. many stocks were not associated with each other with a 0.05 significance level. Five small and strongly associated clusters were evident among the 15 stocks: Prince William Sound and Sitka Sound, Kah Shakes and Prince Rupert, West Vancouver Island and Strait of Georgia, Queen Charlotte Island and central coast of British Columbia. and North Sea and ICES district Via north.

For the high frequency data of Dlog(R), the distances between the large clusters were somewhat longer than the Log(R) data (Figure 2.6). The small and closely associated clusters also included Prince William Sound and Sitka Sound, and North Sea and ICES district Via north. But another three small clusters emerged different from the Log(R) data. Three stocks from neighborhood geographic areas (Queen Charlotte Island. Prince Rupert and Kah Shakes) formed a strong cluster. Three stocks from the central and southern British Columbia (central coast, west Vancouver Island and Strait of Georgia) were linked as another cluster. the eastern Bering Sea stock was associated with the Seymour Canal stock to form a cluster.

Compared with the Log(R) and Dlog(R) data. the major difference with the residuals from LOWESS fits of stock-recruitment data was that the Atlantic stocks were not grouped together other than the Icelandic summer spawning and Norwegian spring spawning stocks (Figure 2.7). Other major differences were that the Kah Shakes stock

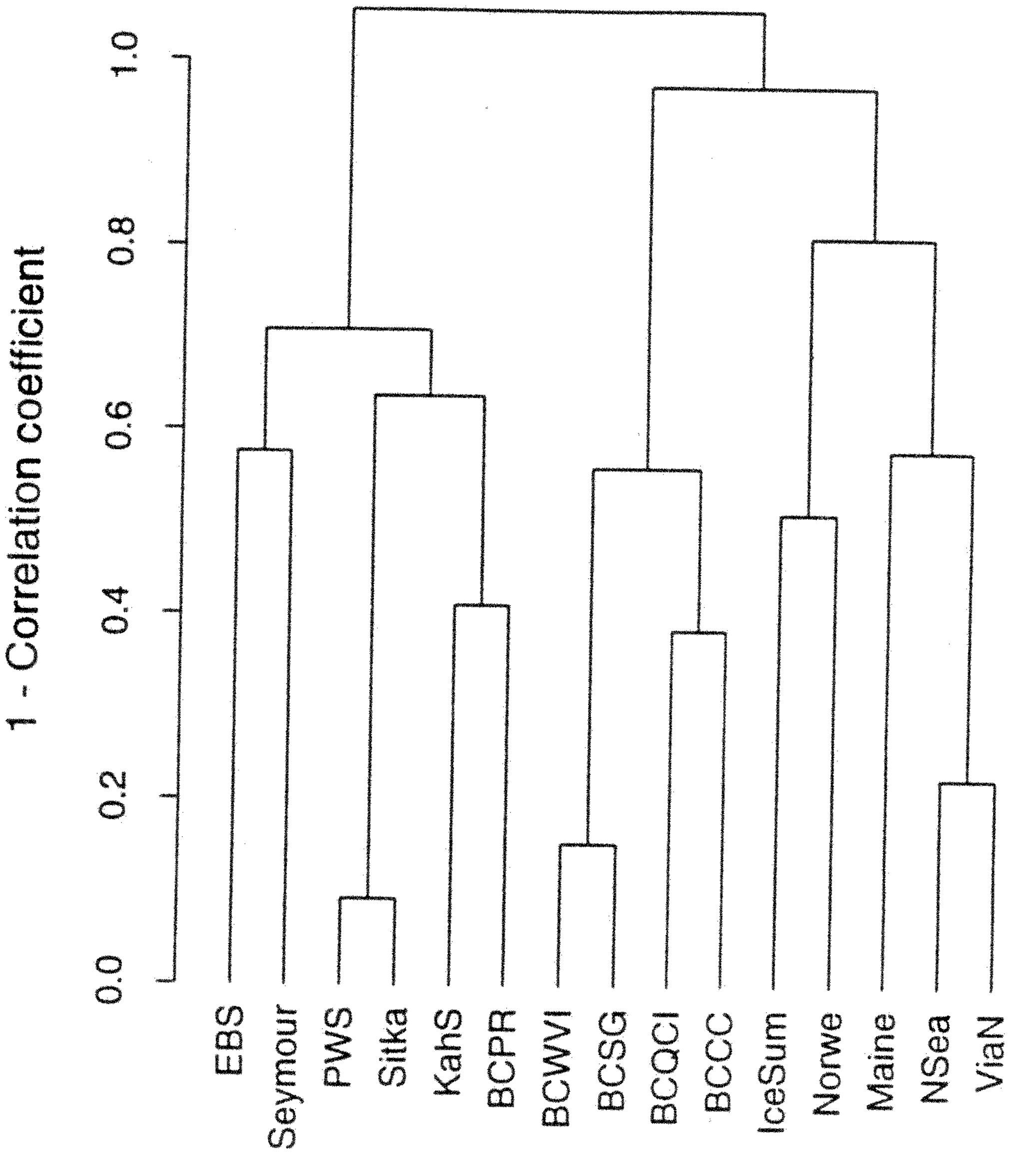

Figure 2.5. Cluster diagram of log-transformed herring recruitment data from 15 stocks in the north Atlantic and northeast Pacific Oceans. Group-average linking was used. See stock notations in Table 2.1.

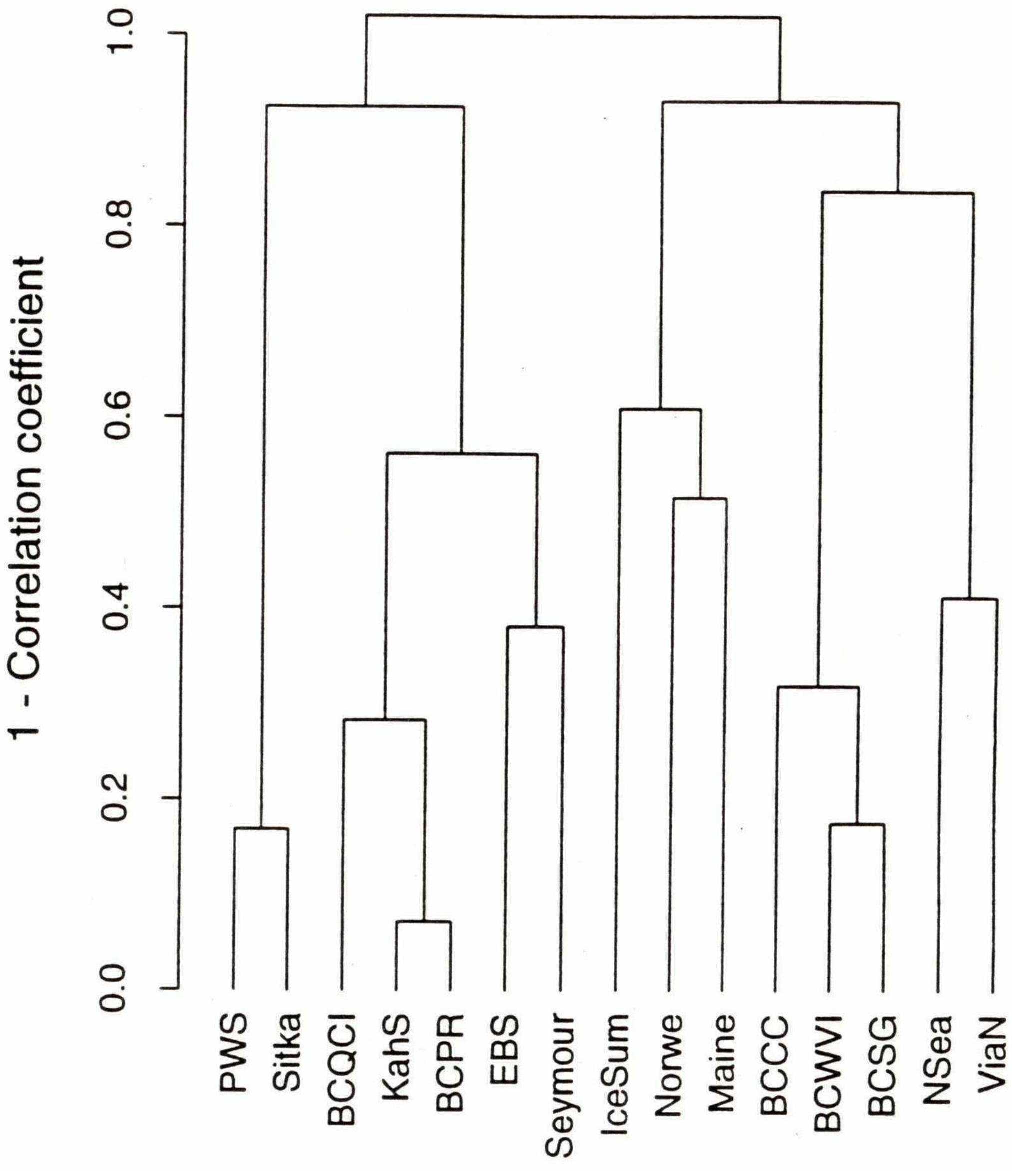

Figure 2.6. Cluster diagram of first-difference of log-transformed herring recruitment data from 15 stocks in the north Atlantic and northeast Pacific Oceans. Group-average linking was used. Sea notations in Table 2.1.

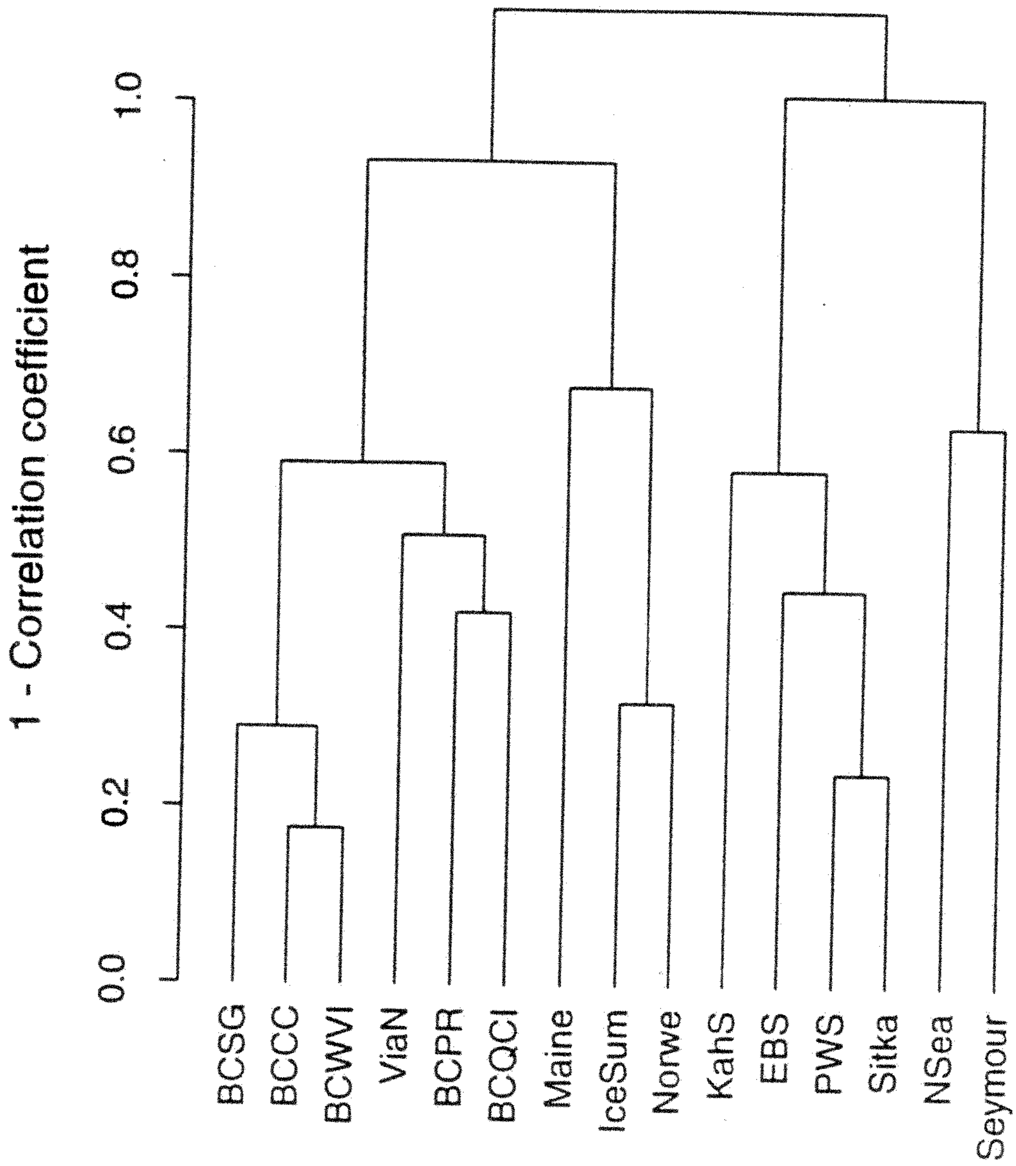

Figure 2.7. Cluster diagram of residuals from LOWESS fitted curves of herring stock-recruitment data from 15 stocks in the north Atlantic and northeast Pacific Oceans. Group-average linking was used. Sea notations in Table 2.1.

did not relate to its neighbor the Prince Rupert stock at all, and that the eastern Bering Sea stock was more closely associated with the Prince William Sound and Sitka Sound stocks. The clusters were more loosely grouped together with the residual data than the Log(R) and Dlog(R) data because the correlations among the stocks were weaker for the residual data than the other two data forms.

Herring recruitment was very variable, with the ratio of maximum to minimum recruitment up to 700 (Table 2.4). With stocks having more than 30 years of data, the strongest year-class was at least 29 times larger than the weakest one. Some stocks, like Icelandic spring spawners, still have not recovered after collapsing about three decades ago. The recruitment distributions of many stocks (3 Newfoundland stocks, Prince William Sound, Sitka Sound, Kah Shakes, Queen Charlotte Island, and central coast of British Columbia stocks) were highly skewed to the strong year-classes and the populations were basically supported by a few stronger-than-average year-classes (Table 2.4). Some stocks, especially the Atlantic stocks, could take up to 17 years to get a stronger-than-average year-class. The variations of year-classes 1970-1986 were generally similar to year-classes 1948-1986 with one exception. The Norwegian spring spawning stock had only one stronger-than-average year-class during 1970-1986. Overall, the recruitment of less variable stocks (North Sea, ICES district Via north, Icelandic summer spawners, Seymour Canal and Strait of Georgia) depended more strongly on spawning biomass than did other more variable stocks (Tables 2.2 and 2.4).

DISCUSSION

Herring, classified by Cushing (1982) as an "environmental type" species, is one of the marine fish species with the most variable recruitment. For such a fish species, is recruitment related to its spawning stock? The answer is definitely yes, at least at low spawning stock levels. It is intuitive that recruits are survivors from the eggs which are spawned by the spawning stock. No eggs will result in no recruits in a closed population. The critical questions are how important are the density-dependent effects on recruitment and whether we can detect them statistically. The results in this study

Table 2.4. Summary of herring recruitment from 19 stocks in the north Atlantic and northeast Pacific Oceans.

	Year-classes 1948-1986						Year-classes 1970-1986					
Stock	Ratio	C.V.	N	Yr	N/yr	Maxyr	Ratio	C.V.	N	Yr	N/yr	Maxyr
1 NSea	51.2	0.71	18	39	2.2	17	35.9	0.91	6	17	2.8	>12
2 ViaN	7.1	0.55	8	17	2.1	6	7.1	0.55	8	17	2.1	6
3 IceSum	41.7	0.74	18	39	2.2	8	15.4	0.74	6	17	2.8	>5
4 IceSpr	12107.0	0.90	9	22	2.4	>30	NA	NA	NA	NA	NA	NA
5 Norwe	620.8	1.57	13	37	2.8	17	168.5	2.73	1	17	17.0	>14
6 Maine	18.5	0.66	8	21	2.6	6	18.5	0.70	6	17	2.8	6
7 WBNDB	169.6	1.41	5	16	3.2	>10	29.6	1.23	4	10	2.5	5
8 BBTB	520.3	2.15	3	16	5.3	>10	31.7	1.26	3	10	3.3	7
9 CBSS	735.3	2.37	4	16	4.0	>10	36.0	1.09	4	10	2.5	5
10 EBS	135.7	0.98	10	31	3.1	>7	135.7	1.18	4	17	4.3	>7
11 PWS	66.9	1.26	5	18	3.6	6	66.9	1.23	5	17	3.4	6
12 Sitka	429.0	1.45	4	19	4.8	>9	429.0	1.36	4	17	4.3	>7
13 Seymour	6.2	0.53	6	14	2.3	>5	6.2	0.53	6	14	2.3	>5
14 KahS	20.2	1.00	4	14	3.5	>5	20.2	1.00	4	14	3.5	>5
15 BCPR	57.2	0.75	14	39	2.8	9	10.2	0.76	5	17	3.4	>8
16 BCQCI	131.7	1.25	10	39	3.9	8	43.4	1.19	6	17	2.8	5
17 BCCC	30.3	0.96	12	39	3.3	9	18.7	1.08	4	17	4.3	8
18 BCWVI	137.2	0.68	15	39	2.6	10	15.2	0.77	6	17	2.8	10
19 BCSG	28.9	0.58	16	39	2.4	10	4.7	0.45	8	17	2.1	6
Average	178.2	1.09			3.2		57.5	0.99			3.6	

Abbreviations:

Ratio: ratio between the strongest to weakest year-classes

C.V.: coefficient of variation of recruitment

N: number of stronger-than-average year-classes

Yr: total number of years with recruitment data

N/yr: average number of years between stronger-than-average year-classes (equal to number of stronger-than-average year-classes divided by total number of years)

Maxyr: maximum number of years between stronger-than-average year-classes (i.e., maximum interval between two stronger-than-average year-classes).

indicate that recruitment from the majority of the 19 herring stocks in the Atlantic and Pacific Oceans is compensatory density-dependent. The survival rates from eggs to recruits decrease as the spawning biomass increases. The relationships between year-class strength and spawning biomass are difficult to detect. These relationships cannot be detected for slightly more than half of the stocks at a 0.05 significance level. Three different statistical tests (2 parametric and 1 non-parametric tests) reach similar conclusions.

As expected, a majority of the stocks have a dome-shaped stock-recruitment curve, with strong recruitment associated with intermediate spawning biomass. Dome-shaped stock-recruitment curves have been reported for several herring stocks worldwide (Cushing 1973), for the herring stock in the Strait of Georgia (Stocker et al. 1985), and for several Newfoundland herring stocks (Winters and Wheeler 1987). The dome-shaped curve may partially result from density-dependent mortality of herring eggs. Herring are demersal spawners with limited spawning grounds due to limited suitable bottom substrate for spawn deposition (Haegele and Schweigert 1985). A large spawning biomass deposits a high density of eggs that result in high egg mortality due to suffocation (Haegele and Schweigert 1985). On the other hand, high egg mortality may result from the low egg density because predation of herring eggs by birds is relatively constant over time (Haegele and Schweigert 1985). Maximum larval production was observed to occur at medium egg densities (Taylor 1971). A detailed discussion on the biological basis of the dome-shaped stock-recruitment curve for herring can be found in Winters and Wheeler (1987).

Stock-recruitment relationships for some herring stocks were neither statistically nor visually apparent. Measurement errors in the estimation of spawning stock and recruitment and stochasticity of actual recruitment due to environmental variation can mask these stock-recruitment relationships (Walters and Ludwig 1981). Current survey methods of herring abundances include aerial, spawn deposition, hydroacoustic and larval trawl surveys (Jakobsson 1985; Trumble and Humphreys 1985), which are prone to different levels of measurement errors. Koslow (1992) demonstrated that a stock-recruitment relationship could not be defined for a fish stock with high fecundity. High fecundity could increase variation of recruitment, which results in difficulty in detecting the stock-recruitment relationship. But high fecundity does not necessarily mask the stock-recruitment relationship for herring stocks, because many herring stocks in this study have similar fecundity and natural mortality, but some of them have well-defined stock-recruitment relationships and others do not.

For a given spawning biomass, stock-recruitment relationships can describe only mean recruitment, which is likely modified by environmental conditions and multi-species interactions. Thus, stock-recruitment relationships are valuable in studying long-term harvest strategies (Walters 1986), but not accurate for short-term forecasts. Spawning stocks and environmental factors are usually combined to examine recruitment dynamics. Wespestad (1991) showed that herring recruitment in the eastern Bering Sea was related to spawning biomass, sea surface temperature and wind-driven transport. Stocker et al. (1985) indicated that spawning stock, sea surface temperature and summer river discharge were important factors in determining year-class strengths of the Strait of Georgia herring. Winters and Wheeler (1987) concluded that much of the recruitment variation of seven herring stocks in Newfoundland could be explained by spawning stock, sea surface temperature and salinity. Although many correlation studies such as the above indicate that recruitment was highly significantly associated with environmental factors, it is an open question whether such correlations are real or spurious. Schweigert and Noakes (1991) showed that stock-recruitment models combined with environmental factors did not improve the recruitment forecast precision of British Columbia herring stocks from the stock-recruitment models without environmental factors. Thus, recruitment-environmental relationships are probably not useful for predicting recruitment. However, recruitment-environmental relationships are useful for factoring out some of the recruitment variation to better reveal the underlying stock-recruitment relationship. For example, the stock-recruitment relationship was not apparent for the Sitka Sound herring stock until the effect of sea surface temperature was removed (Zebdi and Collie *in press*). The relationships between herring recruitment and environmental factors may be far more complex than simple correlation studies reveal.

Herring recruitment variation may also be partially caused by species interactions. Walters et al. (1986) demonstrated that the herring recruitment in the Hecate Strait, British Columbia, is strongly influenced by cod predation. Ware and McFarlane (1986) showed that the herring year-class strengths off the west coast of Vancouver Island are weakly correlated with the biomass of adult Pacific hake. However, the effects of species interactions on herring recruitment from elsewhere have seldom been demonstrated.

Recruitment data transformations (e.g., Log (R)) that emphasize low-frequency variation have stronger correlations between different stocks than the transformations (e.g., Dlog(R)) that emphasize high-frequency variation. After removing the influence of spawning stocks, the data sets have the weakest correlations among these three data sets. These results are consistent with the conclusions by Hollowed et al. (1987) in which correlations among low-frequency data were much stronger than among the high-frequency data. The strong correlations among low-frequency data might be caused by the synchrony of recruitment, autocorrelation of recruitment or by both. Positive autocorrelation with a time lag of one year occurred for some stocks. Taking the first-differences of log-transformed recruitment can increase the reliability of the statistical test (Thompson and Page 1989). Overall, the three data forms shared some common results: significant, positive correlations existed among neighboring stocks for some areas. Since this synchrony could not be explained by spawning biomass, the environmental forcing may be an important factor on herring recruitment within a certain geographic area.

In the north Atlantic Ocean, three oceanic stocks. Icelandic summer spawners, Icelandic spring spawners and Norwegian spring spawners, are not closely related, although they share a common environment during certain periods of life cycles (Jakobsson 1980). Strong recruitment occurred for the Icelandic summer spawners regularly, whereas Norwegian spring spawners took 17 years to produce a strong year-class after the collapse in the late 1960's. Icelandic spring spawners have not recovered after their collapse about three decades ago. It is apparent that local environments and spawning stocks are important regulators of these stocks. The North Sea and ICES district VIa north stocks are neighboring shelf stocks. The recruits of these two stocks are highly correlated, although the recruitment of ICES district VIa north stock is much more variable interannually. Common environmental forces might have influenced these two close stocks, but more than half of recruitment variations for both stocks could be explained by spawning biomass alone. Recruitment dynamics of herring stocks in Newfoundland were comprehensively examined by Winters and Wheeler (1987). Three geographically close stocks in Newfoundland are subjected to the influences of the Labrador Current and highly associated each other (Winters and Wheeler 1987). In addition to environmental conditions, spawning biomass is also an important factor. The environmental forces influencing Newfoundland stocks apparently do not extend to the Gulf of Maine because there is no association between the Gulf of Maine stock and Newfoundland stocks.

For first-differenced data sets in the northeast Pacific Ocean, the Prince William Sound and Sitka Sound stocks are strongly clustered and their populations have primarily been supported by strong recruitment every 4 years since 1976. Zebdi and Collie (*in press*) showed that sea surface temperature significantly influences the year-class strengths for the Sitka Sound stock, but the most crucial issue, the cause of the strong 4-year cycle, has not been found. Since the spawning stocks of these two stocks consist of 5 to 10 age groups and are located separately along the Gulf of Alaska, the most likely mechanism causing the 4-year cycle is the environmental force operating in the Gulf of Alaska. Three stocks in central and southern British Columbia are highly correlated. Between these two groups of herring stocks are located three stocks: Kah Shakes, Prince Rupert and Queen Charlotte Island. These three stocks are not only closely associated each other, but also have some patterns similar to their northern and southern neighboring groups. These three groups of herring stocks are approximately located in three oceanic domains proposed by Ware and McFarlane (1989): the northern group in the Coastal Downwelling domain, the middle group in the Transition Zone and the boundary between the Transition Zone and the Coastal Downwelling domain, and the southern group in the Coastal Upwelling domain and the boundary between Transition Zone and the Coastal Upwelling domain. The different recruitment patterns in these three groups may have been caused by the different environmental forces in three oceanic domains (Ware and McFarlane 1989). These environmental forces and species interactions (Walters et al. 1986; Ware and McFarlane 1986) may be the important factors that result in weak density-dependent effects on the recruitment of many herring stocks along the Gulf of Alaska. The eastern Bering Sea stock is not related to the northern group, but is related to the Seymour Canal stock located on the inside waters geographically close to the Sitka Sound stock. Why the eastern Bering Sea and Seymour Canal stocks are associated is not clear, but about half of recruitment variation of the easter Bering Sea stock and the most of recruitment variations of the Seymour Canal stock could be explained by spawning biomass. The recruitment for Seymour Canal stock may be more influenced by the local environmental conditions than the oceanic domain because it is located in the inside waters.

The results regarding the spatial patterns in the northeast Pacific in this study are somewhat different from the conclusions of Zebdi and Collie (*in press*) and Ware and McFarlane (1989). Ware and McFarlane (1989) clustered three major groups of herring in British Columbia from the recruitment data, and Zebdi and Collie (*in press*) separated them as two groups corresponding to the Coastal Downwelling and the combined Transition Zones and Coast Upwelling by using log-transformed recruitment data. Zebdi and Collie (*in press*) also found a correspondence between these recruitment patterns and sea surface temperature patterns. Besides the different treatment of recruitment data, there are noticeable differences between this study and the past studies (Schweigert et al. 1993): 1) the stock definitions for British Columbia herring have been changed; 2) catch-age analyses for British Columbia herring have been modified to estimate instantaneous natural mortality; and 3) different time series of recruitment data were used. If the whole time series of log-transformed recruitment data are applied, all herring stocks in British Columbia are strongly correlated and no discrimination can be made. By taking first-difference of log-transformed recruitment data, I was able to detect the gradient changes of the herring recruitment patterns among the three oceanic domains. The boundaries of these oceanic domains may shift from year to year and herring may spend some time in other oceanic domains during their life cycles (Ware and McFarlane 1989), which make the stock grouping more of a gradient.

The herring recruitment patterns suggest that spatial scale is an important factor in examining the relationships between environmental conditions and recruitment dynamics. Each environmental process may play an important role in recruitment dynamics of herring within a limited spatial scale. In studying the relationships between the anomalous environmental conditions and synchronous extreme year-classes of several northeast Pacific marine fish stocks, Hollowed (1990) was able to identify environmental conditions for synchronous extreme year-classes of some groundfish stocks, but failed to find environmental patterns for environmental type stocks of pelagic fish. Thus, the environmental influences on recruitment may be large scale for some stocks and on a very limited scale for others.

The density-dependent recruitment for many herring stocks has important implications for herring fisheries management. Many herring stocks have followed boom and bust cycles, and during the last three decades, heavy fishing was followed by the bust cycles of several major herring stocks (Jakobsson 1985; Hourston 1980). Once a stock collapsed, it would take many years to produce a strong recruitment to recover under a low spawning stock (Table 2.5). Some stocks could not recover even after two to four decades. Within a few years after fisheries were closed when stock abundances fell below low levels, many herring stocks began to recover (e.g., the Kamishak Bay stock, Icelandic summer spawners, the North Sea stocks, the West coast of Vancouver Island and Queen Charlotte Island stocks, see Table 2.5). In cases in which no management actions were taken to stop fishing, many stocks have not yet shown signs of recovering since collapses two to four decades ago (e.g., the Icelandic spring spawning and the Hokkaido herring stocks). Although fishery closures may not help all

Table 2.5. Examples of collapse and recovery of herring stocks. Summary of peak spawning biomass during observed period, period of fishery closure, spawning biomass when the fishery closure occurred and when the fishery was re-opened.

Stock	Peak Spawning Biomass (t)	Observed Period	Closed Period	Biomass at Closure (t)	Biomass at Opening (t)
Kamishak Bay, Alaska	28,032	1978-92	1980-84	2,631	11,057
Nelson Island, Alaska	10,000	1978-92	1990-91	2,454	4,785
Queen Charlotte Is., Canada	50,449	1951-92	1968-71	2,712	17,384
West Vancouver Is., Canada	112,700	1951-92	1968-71	8,132	61,240
Icelandic Summer Spawners	313,000	1947-92	1972-74	11,000	119,000
North Sea	3,890,000	1948-92	1977-80	60,000	215,000
Norwegian Spring Spawners	11,150,000	1952-92	1971-83[a]	50,000	590,000
Hokkaido	975,000[b]	1890-1956	1956-NA[c]	NA	NA
Icelandic Spring Spawners	819,000	1947-92	1968-NA[c]	3,300	NA
Lynn Canal, Alaska	11,294	1972-92	1983-present	1,623	1,678[d]

[a]: A small amount of catch quota was allowed for some years. [b]: Total catch. [c]: No management action was taken to close the fishery and the fishing was stopped by fishermen due to low catch; no signs of recovery have been seen for these two stocks. [d]: spawning biomass in 1992; the fishery has been closed since 1983.

Sources: See Table 2.1 for stocks in Canada, North Sea, Iceland and Norway; Bucher and Hammarstrom (1993) for the Kamishak Bay stock; Hamner and Kerkvliet (1992) for the Nelson Island stock; D. Carlile of Alaska Department of Fish and Game (personal communications) for the Lynn Canal stock; and Morita (1985) for the Hokkaido stock.

depressed herring stocks to recover within a short time horizon (e.g., the Lynn Canal stock (Table 2.5)) and favorable environmental conditions also help stock recovery (Corten 1986), prohibiting fishing is one of the most important factors affecting the timing of recovery of a depressed stock. Thus, management strategies for herring fisheries should take into account spawning stocks, and prevent overfishing. One of the most effective management strategies to protect the spawning stocks and prevent overfishing is a threshold management strategy, in which no fishing will be allowed if the stock falls to a low level. The next stage of this study will examine methods defining threshold levels and factors influencing the optimal threshold levels for a given fish stock.

Chapter Three

THRESHOLD MANAGEMENT STRATEGIES FOR EASTERN BERING SEA POLLOCK

SUMMARY

A single-species simulation model of an age-structured population with stochastic recruitment was constructed for eastern Bering Sea (EBS) pollock with a threshold management strategy. Other factors considered were fishing mortality, recruitment, and initial biomass. The objective function was a weighted function of increased average yield and decreased standard deviation of yield over a planning horizon. I used my model to solve two problems. First, I determined the optimal threshold given a prescribed fishing mortality. Second, I determined optimal threshold and fishing mortality, simultaneously. Applied to EBS pollock, a threshold management policy always increased average yield over a non-threshold policy. For the first problem, optimal threshold levels ranged from 20% to 30% of pristine biomass. For the second problem, each scenario had a unique threshold and fishing mortality, with fishing mortality slightly above the maximum sustainable yield (MSY) level and a threshold range of 25-50%. These results were robust with regards to other factors. Benefits of the threshold policy were greater with higher fishing mortality and with a Ricker spawner-recruit model than with a Beverton-Holt model. The success of the threshold management policy is due to the relatively rapid rebuilding of a population to levels producing MSY.

INTRODUCTION

The gadoid fish species walleye pollock, *Theragra chalcogramma* (Pallas 1811), is the only recognized member of the genus *Theragra* and is the most abundant fish species in the northeast Pacific Ocean. In the EBS, the peak abundance of pollock was estimated at 12.6 million t from 1964 to 1987 (Bakkala 1988). Pollock not only supports a huge fishery but also forms one of the most important components of the Bering Sea biological system, representing a large fraction of the total standing stock of EBS demersal fish. The majority of the groundfish catch in the EBS and Aleutian Islands region is pollock (NPFMC 1991).

A comprehensive review of the biology and management of walleye pollock from around the world was presented in a symposium organized by Alaska Sea Grant College Program (1989). Pollock is a semidemersal species, usually forming schools near the bottom during daytime and dispersing up into the water column at night (Smith 1981). In the EBS, the female pollock start to mature at age 2, and the majority of females mature between ages 3 and 6. The spawning period of pollock has been reported to extend from the end of February through July, with peak spawning activity from the middle of March until the middle of May (Smith 1981; Bailey et al. 1986). Cannibalism and predation are important determinants of pollock population dynamics in the EBS (Smith 1981; Bakkala 1988; Honkalehto 1989; Livingston 1989; Mito 1990), although I do not have enough information to make use of those features in my model.

Before 1963, small amounts of pollock in the EBS were occasionally harvested by Japanese trawlers. Because of declining catch rates of yellowfin sole in the Bering Sea, Japanese trawlers began directed pollock fisheries in 1964. After processing techniques were developed to manufacture pollock into Surimi, a traditional Japanese seafood commodity, commercial catches increased rapidly in 1967 and reached a peak in 1970-1975 with catches ranging from 1.3 to 1.9 million tonnes annually. Pollock catches were gradually reduced through bilateral agreements between Japan and the USSR after the peak catch in 1972 (Bakkala et al. 1987). After implementation of the Magnuson Fishery Conservation and Management Act (MFCMA) in 1977, catch quotas have been set from 950,000 tonnes to 1.4 million tonnes since 1977. In 1980, U.S. trawlers began harvesting pollock and by 1990 the pollock fishery was fully Americanized. Figure 3.1 illustrates total pollock catches and population biomass of ages 3-9 in the EBS from 1964 to 1990. Since implementation of MFCMA,

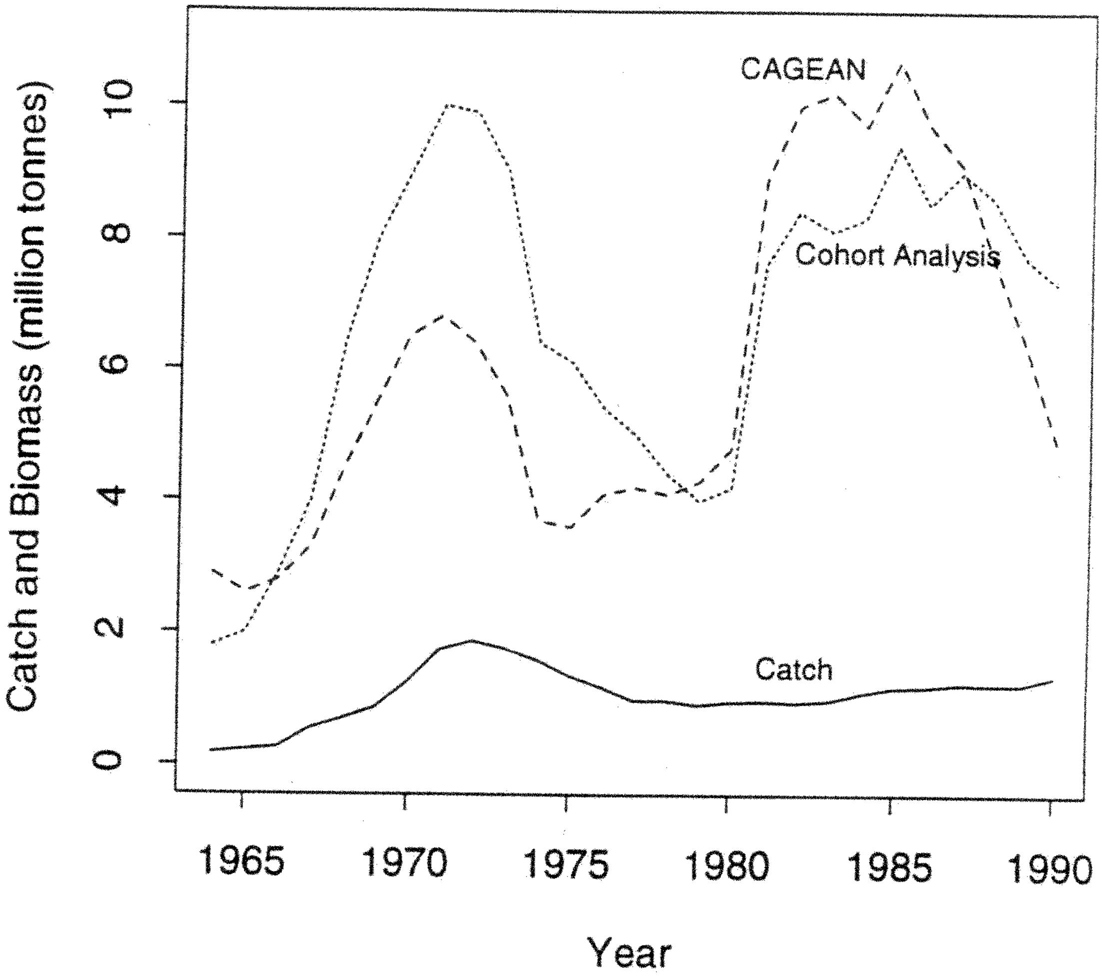

Figure 3.1. Total catch and biomass of ages 3-9 of walleye pollock in the eastern Bering Sea. Two series of biomass were estimated with CAGEAN and cohort analysis, respectively.

conservative harvest rates of around 25% or less have been used.

The population dynamics and management strategies of EBS pollock have been a subject of intensive study during the last two decades. Population dynamics was examined by Chang (1974) with a surplus production model, yield per recruit analysis and cohort analysis. Chang's studies were extended by Low (1974) to multi-species population dynamics. Population dynamics and consequences of harvests were investigated with ecosystem simulation approaches by Laevastu and Favorite (1976), Laevastu and Larkins (1981), and Knechtel and Bledsoe (1983). Wespestad and Terry (1984) used an age-structured population model containing economic functions to study biological and economic yields under differing harvesting regimes. Constant effort and fixed escapement policies were compared for Bering Sea pollock by Getz et al. (1987) through computer simulations. Alternative population models for EBS pollock were examined by Quinn and Collie (1990). None of these studies embedded a threshold level in their population models.

In this chapter (based on Quinn et al. 1990), I analyzed walleye pollock population dynamics in the EBS with an age-structured computer simulation model similar to Deriso et al. (1985) and Quinn (1986) under various threshold rules and investigate the effects of some important factors on each threshold management policy. Optimal threshold levels and fishing mortality rates were determined as a function of average yield and standard deviation of yield. The first optimality problem determined the optimal threshold given a prescribed level of fishing mortality. The second optimality problem determined optimal levels for the threshold and fishing mortality, simultaneously.

METHODS

Data Analysis

Natural mortality, length, weight, fecundity and catch-age data were provided by V. Wespestad (NWAFC, NMFS, NOAA, Seattle WA), covering ages 2 through 9 between 1964 and 1987. Table 3.1 summarizes population parameters. In addition, three

Table 3.1. Estimates of natural mortality, maturity, fecundity and selectivity, and growth and spawner-recruit parameters of eastern Bering Sea pollock. The Beverton-Holt curve was fitted by eye so that standard deviations of estimated parameters and R^2 are not available.

Age	Instantaneous Natural Mortality	Proportion Mature	Fecundity (# of Eggs)	Gear Selectivity
2	0.45	0.008	16200	0.163
3	0.30	0.289	44100	0.474
4	0.30	0.641	77900	1.000
5	0.30	0.842	114000	1.000
6	0.30	0.901	133000	0.990
7	0.30	0.947	169000	0.587
8	0.30	0.963	193000	0.634
9	0.30	0.970	206000	0.694

Growth (kg) model	Spawner-recruit model	
	Ricker	Beverton-Holt
$W_\infty = 1.537$	$\alpha = 0.06211$	0.104274
$k = 0.221$	$\beta = 0.00205$	0.009932
$t_0 = -0.827$	$\gamma = 0.0$	-1.0
$b = 3.353$	$\sigma = 0.47$	NA
	$SD(\alpha) = 0.01844$	NA
	$SD(\beta) = 0.00040$	NA
	$R^2 = 0.61$ (DF=17)	NA

estimates of fishing mortality from combined hydroacoustic trawl surveys were available (0.666 in 1979, 0.152 in 1982, and 0.100 in 1985). Finally, virtual population analysis (VPA) was provided, which involved tuning the procedure with the survey information (Quinn and Collie 1990). Previous analyses of walleye pollock (Alton and Deriso 1983; Wespestad and Traynor 1988) were helpful in model construction.

Population abundance was estimated with catch-age analysis with auxiliary information and the catch-age analysis computer program CAGEAN (Deriso et al. 1985, 1989). Natural mortality was set to 0.45 at age 2 and 0.30 at older ages in accord with other analyses (e.g., Wespestad and Traynor 1988). Age selectivity was set to 1 for ages 4-5, based on results from the VPA procedure. Catch-age analysis was performed by Dr. Terry Quinn of University of Alaska Fairbanks and the methods and results of the catch-age analysis are described by Quinn et al. (1990) and Quinn and Collie (1990).

Figure 3.2 shows the relationship between recruitment (numbers of fish at age 2) and number of eggs (numbers of fish times percent maturity and fecundity). One very strong year-class (1978) is evident. The deviation of the 1978 year-class is thought to be due to environmental variation (Quinn and Niebauer *in press*). Recruitment declines asymptotically with increasing egg number for sufficiently large values of eggs. The three most recent estimates of recruitment (year-classes 83, 84 and 85) are less than expected from the overall pattern. These values are highly uncertain, being based on few observations of each year-class in the commercial fishery. These three data points were excluded from fitting spawner-recruitment functions.

Two common spawner-recruitment models, the Ricker and the Beverton-Holt, were fitted to the data. The Ricker model appears to fit better than the Beverton-Holt model (Figure 3.2). Because the Ricker model was derived from a process in which cannibalism of young fish by older fish results in declining overall spawning potential at high spawner biomass (Ricker 1954; Gulland 1983), the Ricker model seems most appropriate given pollock biology as well, as described in the introduction. Both spawner-recruitment relationships with stochastic variation were used in the simulation study described below, in order to determine if the threshold analysis was affected by

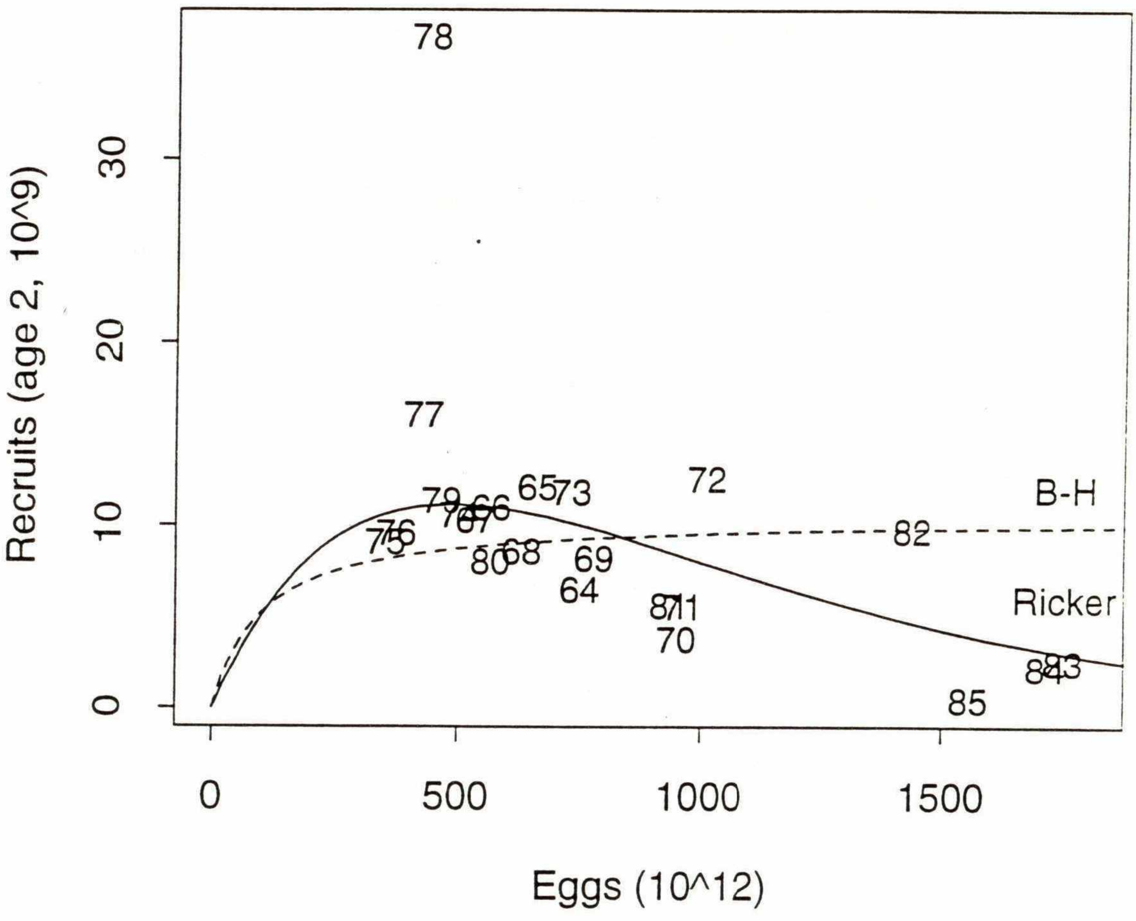

Figure 3.2. Spawner-recruit estimates for each year-class and fits of the Ricker and Beverton-Holt models for eastern Bering Sea walleye pollock. The numbers in the plot are brood-year.

the shape of the spawner-recruitment curve.

Age-structured Model

The age-structured model I used is similar to the one presented by Deriso et al. (1985) and Quinn (1986). The recursion relation of abundance is

(3.1) $N_{t+1,a+1} = N_{t,a} \exp(-Z_{t,a})$

$Z_{t,a} = F_{t,a} + M_a$,

where t stands for year and a for age, $N_{t,a}$ is abundance at the beginning of year t and age a. $F_{t,a}$ is fishing mortality in year t for a-yr-olds, M_a is natural mortality at age a, and $Z_{t,a}$ is total instantaneous mortality in year t and age a. Ages 2 to 9 were modelled. Natural mortality is assumed to be time-independent and fishing mortality separable into an age factor and a year factor,

(3.2) $F_{t,a} = s_a f_t$,

where age selectivity coefficient s_a is equal to 1 for at least one age, and f_t is full-recruitment fishing mortality.

The Baranov catch equation (Ricker 1975),

(3.3) $C_{t,a} = N_{t,a} [1-\exp(-Z_{t,a})] F_{t,a} / Z_{t,a}$,

was used to calculate catches $C_{t,a}$. The biomass and yield were obtained by multiplying weight by age to abundance and catch. The weight w_a is determined by a general von Bertalanffy growth equation (Ricker 1975)

(3.4) $w_a = W_\infty (1 - \exp[-K (a-t_0)])^b$

where W_∞, k, t_0 and b are growth parameters, given in Table 3.1.

The spawner-recruitment relationship is represented in the simulation model by a general model proposed by Deriso (1980):

(3.5) $N_{t,r} = \alpha E_{t-r} (1 - \beta \gamma E_{t-r})^{(1/\gamma)} \exp(v_t)$

where r is the recruitment age, equal to 2 for EBS pollock, $N_{t,r}$ is recruitment in year t, E_{t-r} is number of eggs in year $t-r$, and α, β and γ are parameters. The Ricker and Beverton-Holt models are two special cases of equation (3.5) with γ equal to 0 and -1, respectively (Table 3.1). The random variable v_t is usually assumed to follow a normal distribution with mean 0 and variance σ^2. The term $\exp(v_t)$ is used to represent environmental variation, both for mathematical convenience as well as for biological realism. The theoretical justification for the lognormal distribution is that $\exp(v_t)$ can be interpreted as a random survival factor resulting from many independent and multiplicative environmental factors. The term v_t represents the sum of these random factors, and thus should be approximately normally distributed by the Central Limit Theorem (Walters and Hilborn 1976; Walters 1986). Hennemuth et al. (1980) and Peterman (1981) offer further empirical justification. For the pollock population data (Figure 3.2), the residuals of the Ricker curve are approximately lognormally distributed, although the sample size is too small to allow a rigorous conclusion. The estimated autocorrelation of the residuals for the Ricker model was also small (0.156), suggesting that there was no tendency for good years of recruitment to be followed by either good years or bad years.

Spawning was assumed to occur after fishing so that total numbers of eggs in year t are calculated by

(3.6) $E_t = \sum_a (N_{t,a} - C_{t,a})\, m_a\, f_a$

where m_a is maturity rate at age a and f_a fecundity, given in Table 3.1. This assumption is approximately correct for pollock, for which a significant part of the total harvest is a roe fishery, which directly removes eggs from the annual production.

Simulations

To investigate how the fishery might respond to different threshold management policies should the amount of fish available for harvest decline to low biomass levels, I used the age-structured model for numerical experiments in which the kind and amount of fishing, the management policy, and the assumed characteristics of the pollock stock were varied. I examined the fishery when managed at different threshold values ranging from 0 (no threshold used) to the biomass level producing MSY. The threshold level was expressed as a percentage of pristine biomass. Fourteen threshold levels (0, 5%, 7.5%, and 10% to 60% for each 5% increment) were evaluated for searching optimal levels. The simulated fish stock experienced fishing mortality along with naturally-occurring environmental variation. Each of several factors that might affect the fishery was varied in the simulation to see its effects and how it interacted with other factors to affect yield, variation in yield, rebuilding time, time of first upcrossing of the threshold level and total time below the threshold level (no fishing). The rebuilding time is defined as total number of years for the population starting from the initial biomass to reach its equilibrium biomass level. The factors considered are:

1. Environmental variation v_t, equation (3.5): I used two levels of environmental variation. LOW variation is equivalent to one strong year-class (10 times average year-class size) every 100 years (standard deviation $\sigma = 0.5$), the current best estimate for EBS pollock (Table 3.1). HIGH variation is equivalent to one strong year-class every 10 years ($\sigma = 1.0$). Recruitment variation this high has been observed for some marine fish stocks (Rothschild 1986).

2. Environmental autocorrelation (AC): The tendency of "good" years for recruitment to follow each other in time. I assumed three cases: NO autocorrelation (a good year is as likely to be followed next year by another good year as it is by a bad year), NEGATIVE autocorrelation -0.5 (a good year tends to be followed by a bad one), and POSITIVE autocorrelation 0.5 (good years tend to be followed by good ones, and bad years by bad ones).

3. Fishing mortality: I used LOW fishing mortality equivalent to full fishing mortality rate at MSY from the age-structured model in the absence of environmental variation ($v_t = 0$). HIGH fishing mortality was set at 1.5 times the LOW fishing mortality rate.

4. Planning horizon, the number of years for the simulation: I used a SHORT (20-yr) and a LONG (50-yr) horizon. It is recognized that even the SHORT horizon is much longer than those conventionally in effect when resource policy is driven solely by economic or political considerations.

5. Spawner-recruit relationship: I used RICKER and BEVERTON-HOLT models.

6. Reproductive potential α in equation (3.5): the maximum potential recruits that an individual fish is capable of producing under ideal conditions. I assumed three levels -- MEDIUM (the level actually estimated from the EBS pollock data, Table 3.1), a LOW level half this value, and a HIGH level 1.5 times the MEDIUM value for the Ricker model. This parameter was not varied for the less-likely Beverton-Holt model, due to the large number of other factors considered.

7. Initial biomass: I assumed that the stock had been reduced to 5% or alternatively to 15% of its pristine biomass at the beginning of each computer experiment.

A particular combination of the seven factors is called a scenario. All 192 possible scenarios were simulated. Numerical experiments using the model involved simulated variation in the environment. For this reason, averages and variance around averages for a given set of conditions were calculated from a sufficiently large number of replicate computer runs (5000 for scenarios with environmental autocorrelation and 2000 for the other scenarios) to make the estimates of averages and variances statistically valid.

The simulations are straight forward. For each scenario, I started the simulation from an initial biomass (Figure 3.3). During each fishing season, if the biomass was above the threshold, fishing was allowed; otherwise the fishery was closed. Then the population was updated to next year. If at the end of the duration (planning horizon), the next replicate would be simulated until all replicates were done (Figure 3.3).

Threshold Levels and Optimality Criteria

Common objective functions for determining optimal harvest strategies include the sum, discounted sum, average or median of yield, natural logarithm of yield, or a power function of yield (Ruppert et al. 1984; Deriso 1985; Hightower and Grossman 1987; Getz and Haight 1989). Ideally, management of a fishery should increase yield as well as decrease variation in yield. However, it is possible that a management policy will increase both yield and its variation, leading to an optimization problem with two

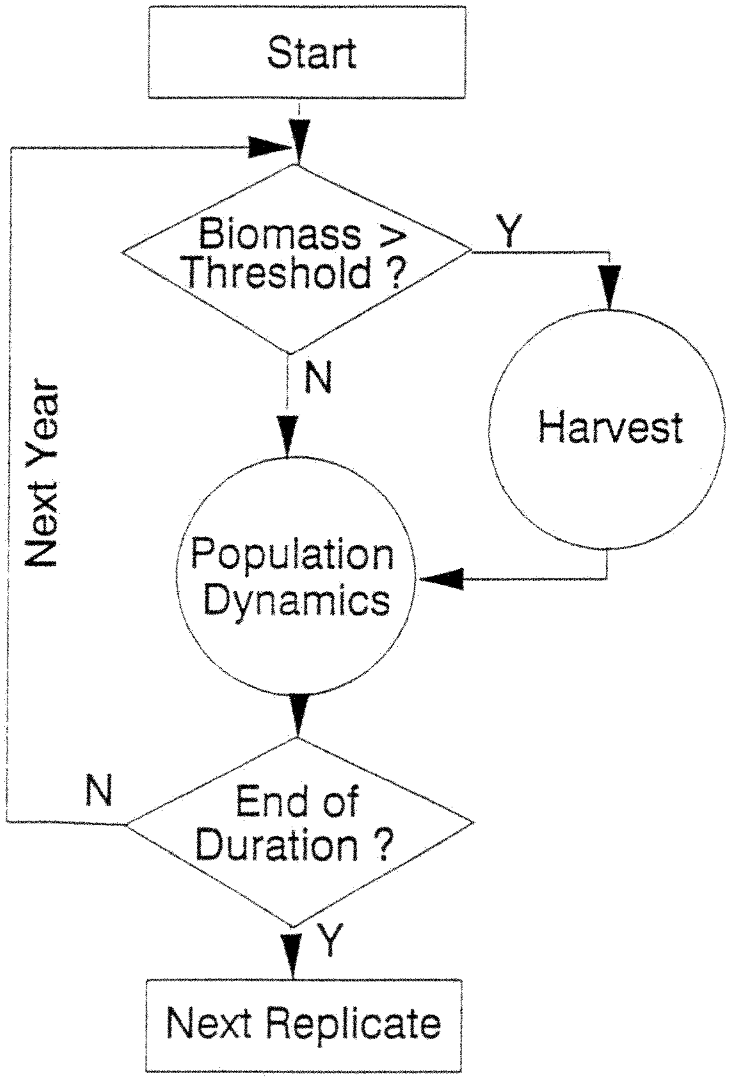

Figure 3.3. Flow chart of computer simulations to evaluate threshold management strategies for eastern Bering Sea pollock.

payoff functions (e.g. Ho 1970). Some trade-off between increased yield and decreased variation in yield is needed to select an optimal threshold level. I chose a flexible objective function of a linear combination of average yield and standard deviation of yield to provide this trade-off. The goal is to maximize the objective over the planning horizon, or

$$(3.7) \qquad \max[(1 - \lambda)\ Y_{th} - \lambda\ SD_{th}]$$

where Y_{th} and SD_{th} is the average annual yield and standard deviation under threshold management policy "*th*", and λ is a penalty weighting factor which measures the cost of one unit of increase in variation in yield in term of a unit of increase in yield. With $\lambda = 0.5$, an equal trade-off of increased average yield with decreased standard deviation is made. Two special cases of objective functions are maximum yield and minimum variation in yield, which correspond to λ equal to 0 and 1, respectively. I also examined the objective of maximum logarithm of yield for some simulations and found that the results were similar to objective function (3.7) with λ approximately equal to 0.2.

Two optimality problems were considered. First, optimal threshold levels were determined under a given level of fishing mortality rate from objective function (3.7). Two levels of fishing mortality rates, LOW and HIGH, were conditioned for the first optimality problem. Examining this problem provides advice regarding implementing a threshold level while continuing the current management practice of setting ABC with a constant mortality rate policy. Current practice determines fishing mortality from either the $F_{0.1}$ or F_{MSY} approach, depending on population status (see NPFMC (1991) for its use with pollock).

Secondly, optimal combinations of threshold levels and fishing mortality rates were determined, using objective function (3.7). This two-parameter optimization problem was investigated to determine if there is a joint solution for finding the optimal fishing mortality and threshold level for a given population, and to examine the sensitivity of this combination to the other factors.

RESULTS

A deterministic age-structured model with the population parameters in Table 3.1 was iterated for a long enough period to determine associated equilibrium biomass and yield as a function of fishing mortality. For the purpose of this study, the pristine biomass for EBS pollock was defined as the maximum equilibrium biomass without fishing under deterministic environmental conditions. The pristine biomass, maximum equilibrium yield and its associated equilibrium biomass were obtained for the Ricker model with three levels of reproductive potential α (equation 3.5) and for the Beverton-Holt model (Table 3.2). The parameters were sensitive to the spawner-recruit model and increased with increased reproductive potential.

The simulations with stochastic variation in recruitment were then made for the scenarios listed above. Average and median yield and the standard deviation of yield over the planning horizon were computed for each simulation and averaged over replicates. Median yield results are not presented, because they did not differ qualitatively. Although absolute levels of average yield and standard deviation of yield varied appreciably among scenarios, the same qualitative conclusions were found regarding the utility of threshold management policies. For all scenarios, average yield increased as a function of the threshold value to a maximum value and then decreased slightly. The standard deviation generally increased as well. As expected, the spawner-recruit model, reproductive potential and environmental variation in recruitment had the largest effects on average yield and standard deviation of yield, because these factors affect average recruitment.

The benefits of introducing a threshold level with the Ricker model with medium reproductive potential, the most likely case for the pollock population, are illustrated in Figure 3.4. The plot shows 24 different simulation scenarios with 5% of pristine biomass as initial biomass. The scenarios are identified by four factors: fishing mortality, environmental variation, planning horizon and environmental autocorrelation. For each scenario, the results are shown for different levels of thresholds, varied from 0 (no threshold) to 60% of the pristine biomass.

Table 3.2. Pristine biomass B_∞, biomass B_{MSY} at maximum sustainable yield (MSY) and its percentage of pristine biomass, MSY, in millions of tonnes, and fishing mortality F_{MSY}, in yr^{-1}, for three different levels of the productivity parameter α for the Ricker spawner-recruit model and one level of the Beverton-Holt model.

	Ricker			Beverton-Holt
Parameter	$\alpha = 0.03$	$\alpha = 0.0621$	$\alpha = 0.09$	$\alpha = 0.1043$
B_∞	5.99	10.42	16.77	13.83
B_{MSY}	3.88	6.36	8.04	6.12
B_{MSY}/B_∞	66%	61%	47%	44%
MSY	0.57	1.30	1.86	1.00
F_{MSY}	0.27	0.42	0.51	0.31

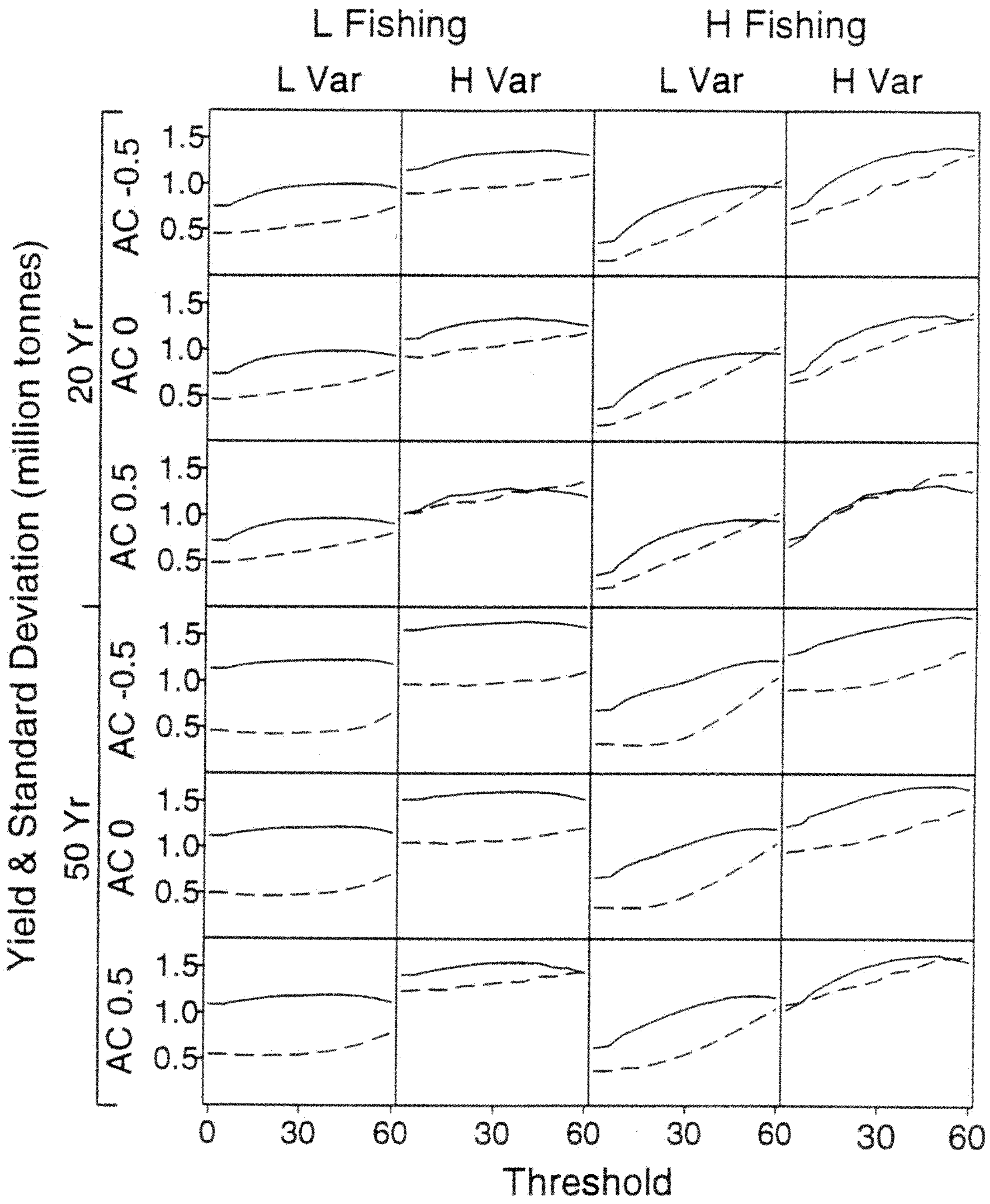

Figure 3.4. Mean yield (solid lines) and standard deviation of yield (dashed lines) as a function of threshold level of 0-60% of pristine biomass for 24 scenarios with 5% initial biomass and medium reproductive potential, α, for the Ricker model. The scenarios are classified by four factors: fishing mortality (LOW: L Fishing, HIGH: H Fishing), environmental variation (LOW: L Var, HIGH: H Var), planning horizon (20-yr, 50-yr) and environmental autocorrelation (-0.5, 0, 0.5).

Under the low fishing mortality scenarios, the increase in yield was of order 10-30%; under high fishing mortality scenarios the increase was of the order 40-170% (Figure 3.4, Table 3.3). For scenarios with high fishing, a threshold management policy provided an opportunity to reduce the fishing effort and keep the population near high reproductive levels. Yield thus increased dramatically. But the increase in the standard deviation beyond a certain threshold level (about 20-30%) was usually more than the increase in yield. In contrast, at the threshold level corresponding to the maximum yield, the increase in yield was often larger than the increase in the standard deviation under scenarios with low fishing.

Of the other factors shown in Figure 3.4, environmental variation had the most effect on average yield: the greater the level of environmental variation, the higher the average yield. This effect occurred because higher environmental variation increased the likelihood of a strong year-class and thus increased average recruitment. Nevertheless, the trend in yield as a function of threshold level was similar under scenarios with high and low levels of noise.

Other factors showed lesser effects, but some are notable. Average yields did not differ appreciably in the scenarios with three different levels of autocorrelation of environmental variation. But the variation in yield was affected greatly, especially in concert with the high level of environmental variation. In this case, standard deviation with negative autocorrelation in recruitment was much less than that assuming positive autocorrelation. Under scenarios with a 20-year planning horizon, the increase in yield was more than that with a 50-year planning horizon. The coefficient of variation of yield also was much larger in scenarios with a 20-year horizon than in scenarios with a 50-year horizon. This is intuitive because the threshold management policy played an important role mainly during the rebuilding period of a population, and 20 years or less were required for the simulated population to rebuild.

This set of 24 scenarios was repeated using the Beverton-Holt model (Figure 3.5). There were two main differences in yield and standard deviation between the Ricker model and the Beverton-Holt model under all scenarios. First, although the

Table 3.3. Optimal threshold levels for combinations of the five factors under low and high fishing mortalities; associated percentages of increased averaged yield, increased standard deviation, and decreased rebuilding times over a policy with no threshold; and number of years of no fishing. Results are given for a penalty weighting factor λ of 0.5.

Scenario					Low fishing mortality					High fishing mortality				
S	I	E	P	AC	T	%Y	%SD	%Rb	<T	T	%Y	%SD	%Rb	<T
R	5	L	20	-0.5	25	27.7	16.0	25.0	4	25	119.8	168.3	75.0	4
R	5	L	20	0	25	28.7	17.6	35.3	4	20	104.9	129.6	65.0	4
R	5	L	20	0.5	25	31.2	21.6	29.4	4	20	110.2	120.4	65.0	4
R	5	L	50	-0.5	25	7.5	-6.3	31.3	4	25	39.7	4.6	80.8	4
R	5	L	50	0	25	7.6	-4.4	31.3	4	25	47.1	18.5	76.0	5
R	5	L	50	0.5	30	8.6	-0.9	35.3	4	30	69.0	46.1	82.1	8
R	5	H	20	-0.5	30	17.3	8.2	27.3	4	25	67.2	53.9	58.3	4
R	5	H	20	0	25	17.6	10.2	27.3	3	20	63.6	46.6	53.8	3
R	5	H	20	0.5	25	22.4	12.4	30.8	4	20	69.6	44.8	60.0	4
R	5	H	50	-0.5	20	4.0	-1.7	27.3	3	35	24.2	9.9	58.3	6
R	5	H	50	0	30	5.6	1.9	27.3	4	25	25.4	10.2	61.5	5
R	5	H	50	0.5	25	9.0	5.7	30.8	5	30	47.3	26.3	66.7	10
R	15	L	20	-0.5	30	6.8	9.9	18.2	2	25	26.6	69.8	75.0	2
R	15	L	20	0	30	7.2	10.5	27.3	2	25	30.6	74.1	72.7	2
R	15	L	20	0.5	25	6.2	7.1	9.1	1	25	35.6	64.9	75.0	3
R	15	L	50	-0.5	30	2.1	1.0	18.2	2	25	11.6	11.8	72.7	2
R	15	L	50	0	30	2.5	1.2	27.3	2	25	16.6	20.3	72.7	3
R	15	L	50	0.5	30	2.8	2.0	25.0	2	30	33.1	39.9	75.0	6
R	15	H	20	-0.5	25	2.0	-2.2	14.3	1	20	11.7	9.0	40.0	1
R	15	H	20	0	25	3.3	1.3	14.3	1	25	21.0	21.6	40.0	2
R	15	H	20	0.5	20	4.7	4.9	12.5	1	15	13.2	9.4	16.7	1
R	15	H	50	-0.5	30	1.6	0.6	14.3	1	30	8.6	5.4	40.0	3
R	15	H	50	0	25	1.3	-1.4	14.3	1	30	14.5	9.7	40.0	4
R	15	H	50	0.5	25	3.6	2.1	25.0	3	30	27.0	17.8	50.0	8
B	5	L	20	-0.5	15	4.3	4.1	8.3	2	15	10.4	10.4	23.1	2
B	5	L	20	0	15	4.4	4.3	8.3	2	15	11.3	11.4	30.8	2
B	5	L	20	0.5	15	4.5	4.4	8.3	2	15	12.8	14.0	23.1	2
B	5	L	50	-0.5	20	1.8	1.3	16.7	3	15	3.5	-1.5	23.1	2
B	5	L	50	0	15	1.5	0.0	8.3	2	15	3.7	0.2	30.8	2
B	5	L	50	0.5	15	1.3	0.0	8.3	2	15	5.0	2.9	23.1	2

Table 3.3 (continue)

Scenario					Low fishing mortality					High fishing mortality				
S	I	E	P	AC	T	%Y	%SD	%Rb	<T	T	%Y	%SD	%Rb	<T
B	5	H	20	-0.5	25	5.7	4.5	25.0	3	20	10.5	7.8	37.5	3
B	5	H	20	0	15	3.9	1.4	12.5	2	20	11.0	11.4	37.5	3
B	5	H	20	0.5	15	3.6	2.0	11.1	2	15	11.5	9.8	22.2	3
B	5	H	50	-0.5	30	2.2	1.2	25.0	3	20	3.7	1.0	37.5	3
B	5	H	50	0	15	1.6	1.0	12.5	2	15	2.7	1.0	25.0	2
B	5	H	50	0.5	15	1.1	-0.1	11.1	2	15	5.5	1.5	33.3	4
B	15	L	20	-0.5	0	0.0	0.0	0.0	0	7.5	0.2	0.1	0.0	0
B	15	L	20	0	7.5	0.0	-0.4	0.0	0	7.5	0.0	-0.5	0.0	0
B	15	L	20	0.5	7.5	-0.2	-1.2	0.0	0	0	0.0	0.0	0.0	0
B	15	L	50	-0.5	10	0.1	0.2	0.0	0	5	0.0	-0.7	0.0	0
B	15	L	50	0	5	0.3	-0.6	0.0	0	15	0.3	0.7	12.5	0
B	15	L	50	0.5	7.5	0.3	0.2	0.0	0	15	1.0	1.5	12.5	0
B	15	H	20	-0.5	15	0.5	-0.5	0.0	0	7.5	0.3	-2.7	0.0	0
B	15	H	20	0	5	-0.2	-2.4	0.0	0	5	0.0	-1.2	0.0	0
B	15	H	20	0.5	5	0.0	-1.7	0.0	0	0	0.0	0.0	0.0	0
B	15	H	50	-0.5	25	0.7	-0.9	0.0	1	20	0.7	-0.8	25.0	1
B	15	H	50	0	15	-0.4	-1.6	0.0	0	15	0.4	-0.8	0.0	1
B	15	H	50	0.5	5	-0.8	-3.8	0.0	0	20	3.8	3.6	20.0	4

Abbreviations:
S: Spawner-recruit curve: Ricker (R) & Beverton-Holt (B).
I: initial biomass (%).
E: environmental variation: LOW (L) & HIGH (H).
P: planning horizon (yr).
AC: environmental autocorrelation.
T: threshold level (%).
%Y: percentage of increase in average yield over not using a threshold.
%SD: percentage of increase in standard deviation of yield.
%Rb: percentage of decrease in rebuilding time.
<T: total number of years of no fishing.

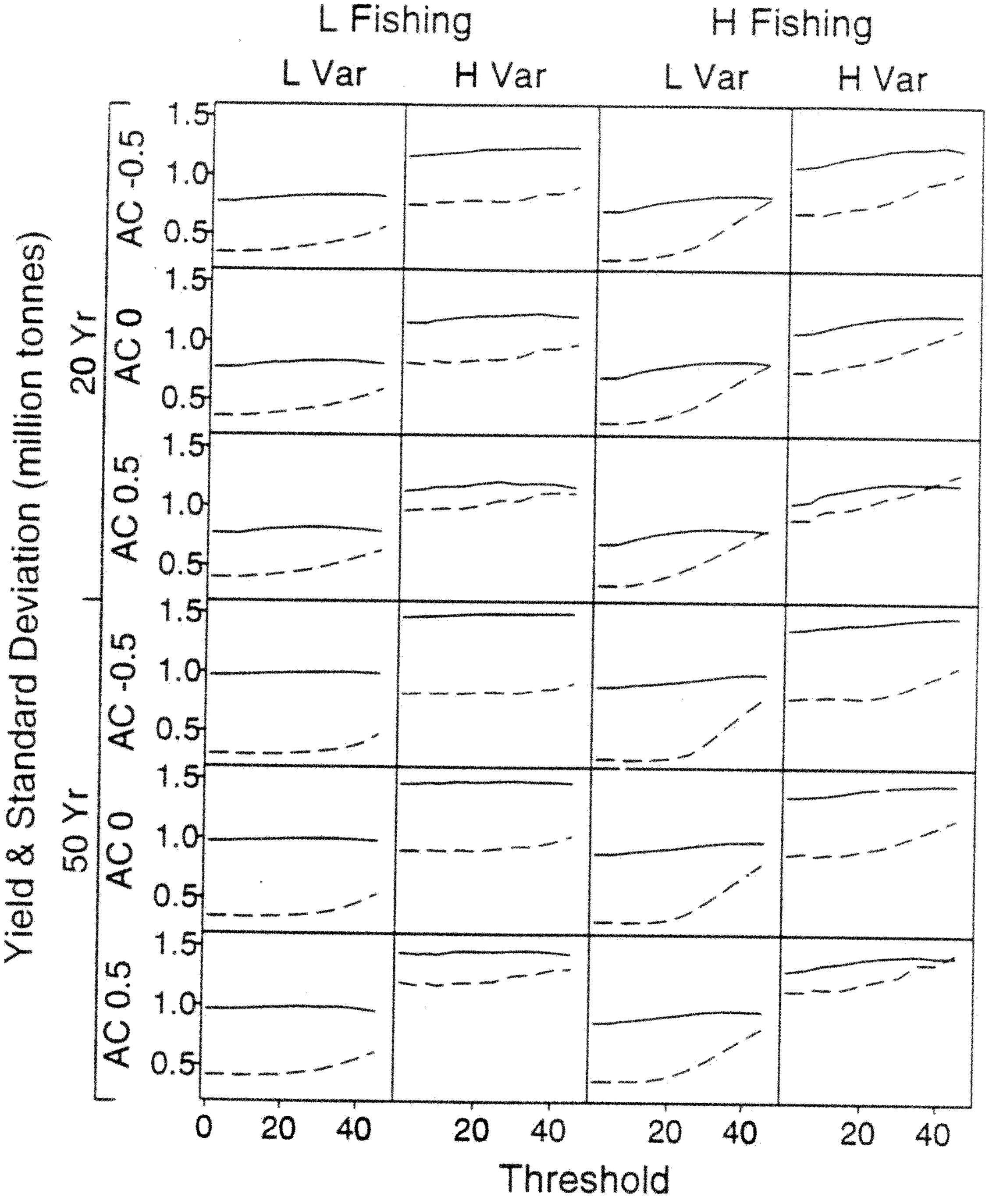

Figure 3.5. Mean yield (solid lines) and standard deviation of yield (dashed lines) as a function of threshold level of 0-60% of pristine biomass for 24 scenarios with 5% initial biomass and the Beverton-Holt model. The scenarios are classified by four factors: fishing mortality (LOW: L Fishing, HIGH: H Fishing), environmental variation (LOW: L Var, HIGH: H Var), planning horizon (20-yr, 50-yr) and environmental autocorrelation (-0.5, 0, 0.5).

average and median yield increased as a function of the threshold value to a maximum yield and then decreased, the increase in yield was very minor. Because the Beverton-Holt curve is asymptotic, it matters less to average yield whether spawning stock varies from the population biomass associated with MSY than a dome-shaped Ricker curve does. Under low fishing scenarios the maximum increase in yield was less than 10%; under scenarios with high fishing the maximum increase was of order 10-20% (Figure 3.5, Table 3.3). Secondly, in each scenario, there existed a threshold level over which the standard deviation of yield increased quickly as the threshold level increased. This breakpoint changed from scenario to scenario and was lower under scenarios with high fishing than with low fishing. The second difference was more apparent under scenarios with low level of environmental variation than with high level of environmental variation.

Median rebuilding time is most usefully illustrated with scenarios using LOW fishing mortality and a 50-year planning horizon (Figure 3.6). For HIGH fishing mortality the population would never rebuild to the level corresponding to the MSY. Scenarios with a 20-yr planning horizon had similar results for rebuilding time, but there are enough scenarios in which the population did not rebuild to reduce confidence in the rebuilding time results. As expected, times to rebuild to high productivity under threshold management were always shorter, and often much shorter, than times to rebuild with no threshold imposed (Figure 3.6). Higher threshold levels produced shorter rebuilding times; cessation of fishing below the threshold allowed the population to increase rapidly when good recruitment occurred. Rebuilding times under scenarios with the Beverton-Holt model were much shorter than those with the Ricker model because the population is required to rebuild to only 44% of pristine biomass for the Beverton-Holt model, compared to 61% for the Ricker model. Median rebuilding times were shorter with higher environmental variation, because the high level of environmental variation produced an occasional strong year-class which rebuilt the population. Generally, the rebuilding times slightly increased under scenarios with environmental autocorrelation changing from negative to positive. Though not shown in Figure 3.6,

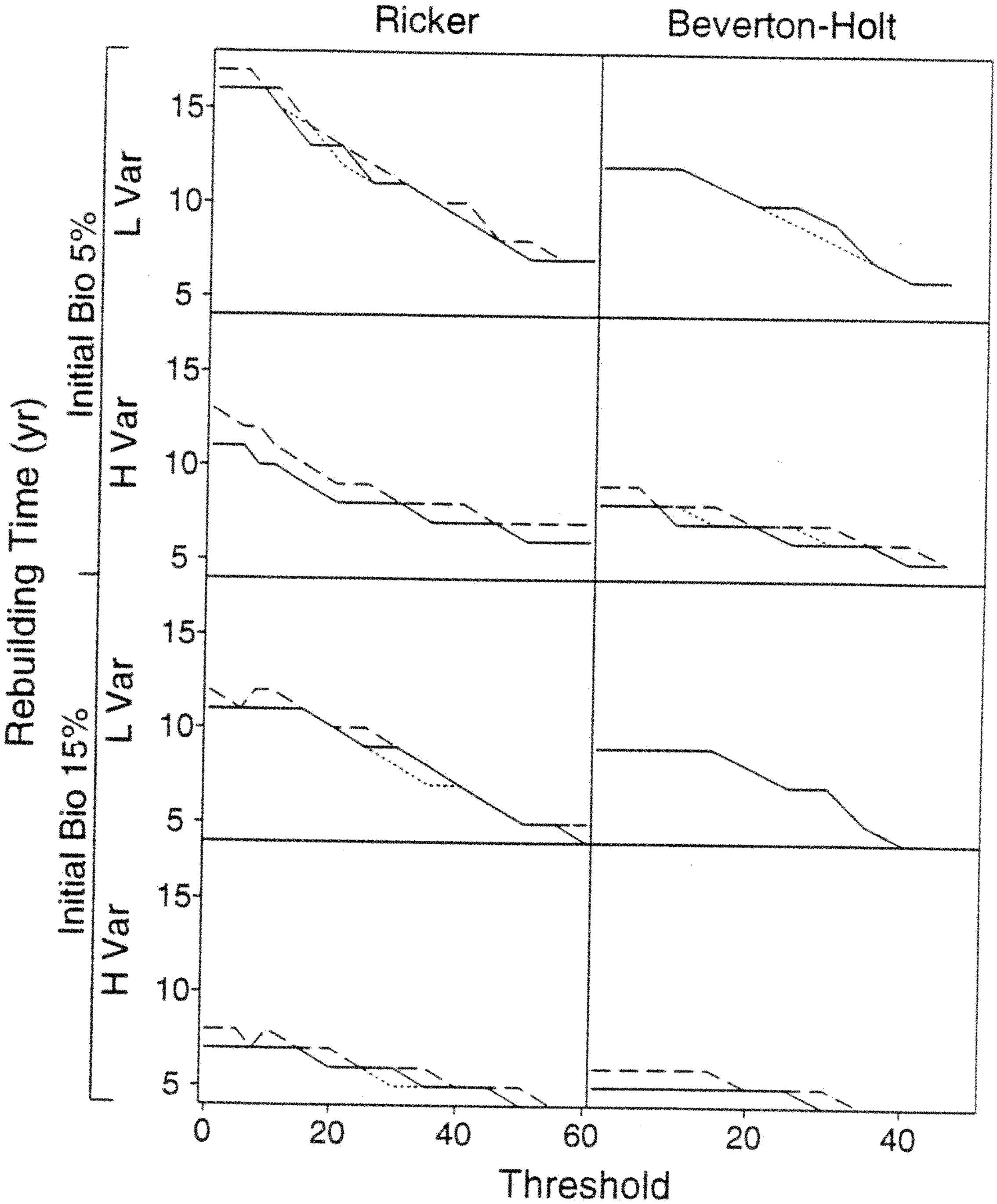

Figure 3.6. Median rebuilding time for scenarios with low fishing mortality and a 50-year planning horizon, classified by four factors: spawner-recruitment model (Ricker with medium α, Beverton-Holt), initial biomass (5%, 15%), environmental variation (LOW: L Var, HIGH: H Var) and environmental autocorrelation (solid lines for -0.5, dotted lines for 0, dashed lines for 0.5).

higher reproductive potential allowed the stock to rebuild more quickly, but the population was much more variable.

Overall, for high levels of the threshold (>25%) the rebuilding time was on the order of 5-10 years; for low values of the threshold (<25%) the rebuilding time was on the order of 10-20 years (Figure 3.6). Rebuilding time itself is a random variable because recruitment is stochastic. The probability distribution of rebuilding time was strongly skewed, which is why I chose median over average rebuilding time. The simulated stock under many scenarios took far longer to rebuild than the median rebuilding time.

Another way to examine the effects of introducing a threshold level on a fishery is to estimate how often the fishery would be closed. Figure 3.7 shows the median percentage of years without fishing under scenarios with LOW fishing mortality and a 50-yr planning horizon. As expected, the percentage of years of no fishing increased quickly as the threshold level increased. The maximum percentage was 36%. For a threshold level less than 30%, fishing was not allowed about 10% of the time or less. The Ricker and Beverton-Holt models had a similar pattern. Environmental autocorrelation had an important influence on the percentage of years without fishing: the percentage is much higher with positive autocorrelation than with negative autocorrelation, especially when combining with high environmental variation. Lower initial biomass resulted in higher percentage of years without fishing. After the population had rebuilt, it rarely dropped below 20% of pristine biomass.

Optimization of Threshold Level

The optimal threshold level for a given penalty weighting factor λ was determined for each scenario by comparing the objective function values among the 14 threshold levels (0-60% of pristine biomass). Figure 3.8 illustrates the trade-off between an increase in average yield and a decrease in standard deviation for selecting optimal threshold levels under all scenarios. The trade-off was measured by the value of penalty weighting factor λ: when λ was equal to 0.5, the same weight was put on both increases

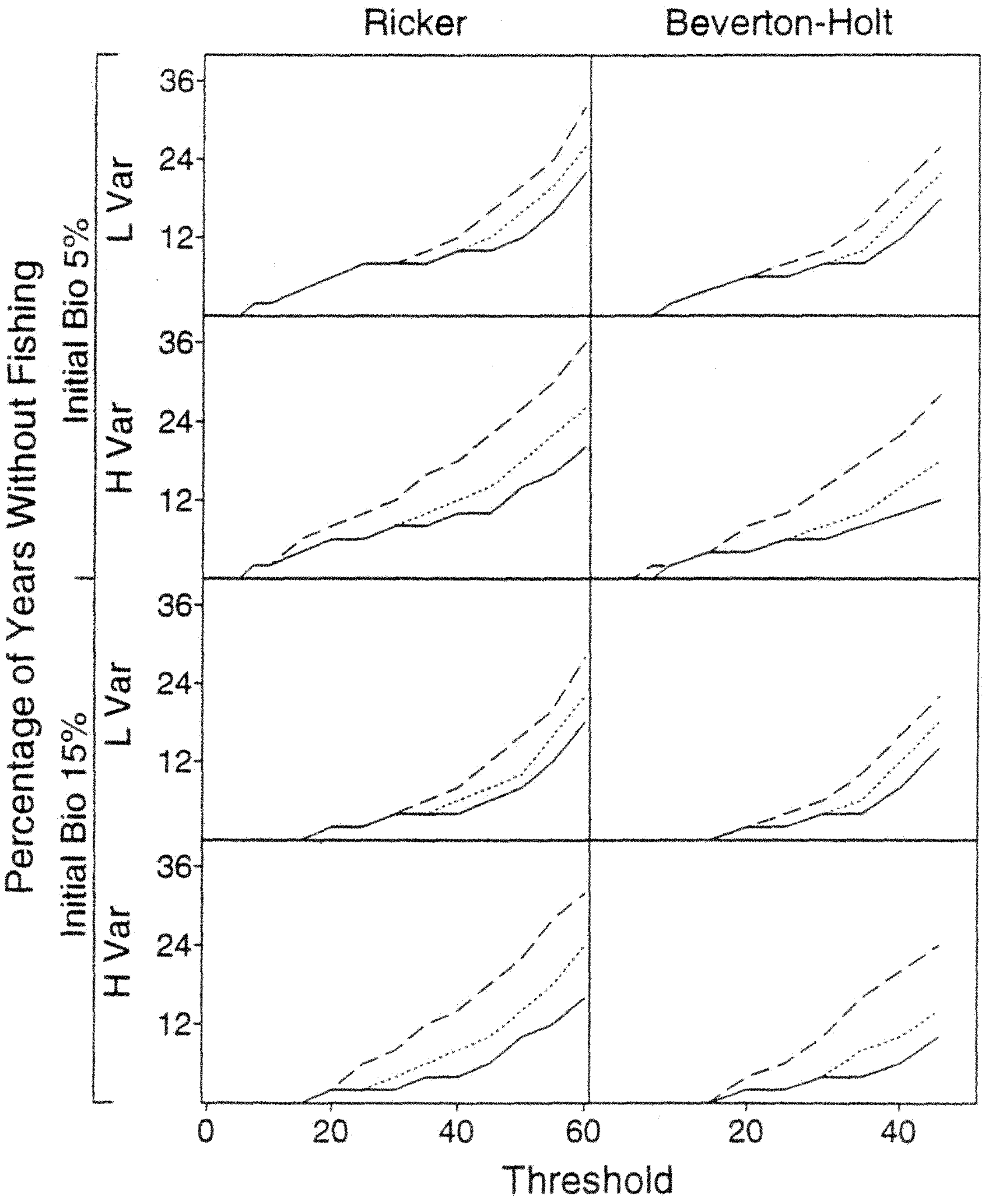

Figure 3.7. Percentage of years of no fishing with low fishing mortality and a 50-year planning horizon, classified by four factors: spawner-recruitment model (Ricker with medium α, Beverton-Holt), initial biomass (5%, 15%), environmental variation (LOW: L Var, HIGH: H Var) and environmental autocorrelation (solid lines for -0.5, dotted lines for 0, dashed lines for 0.5).

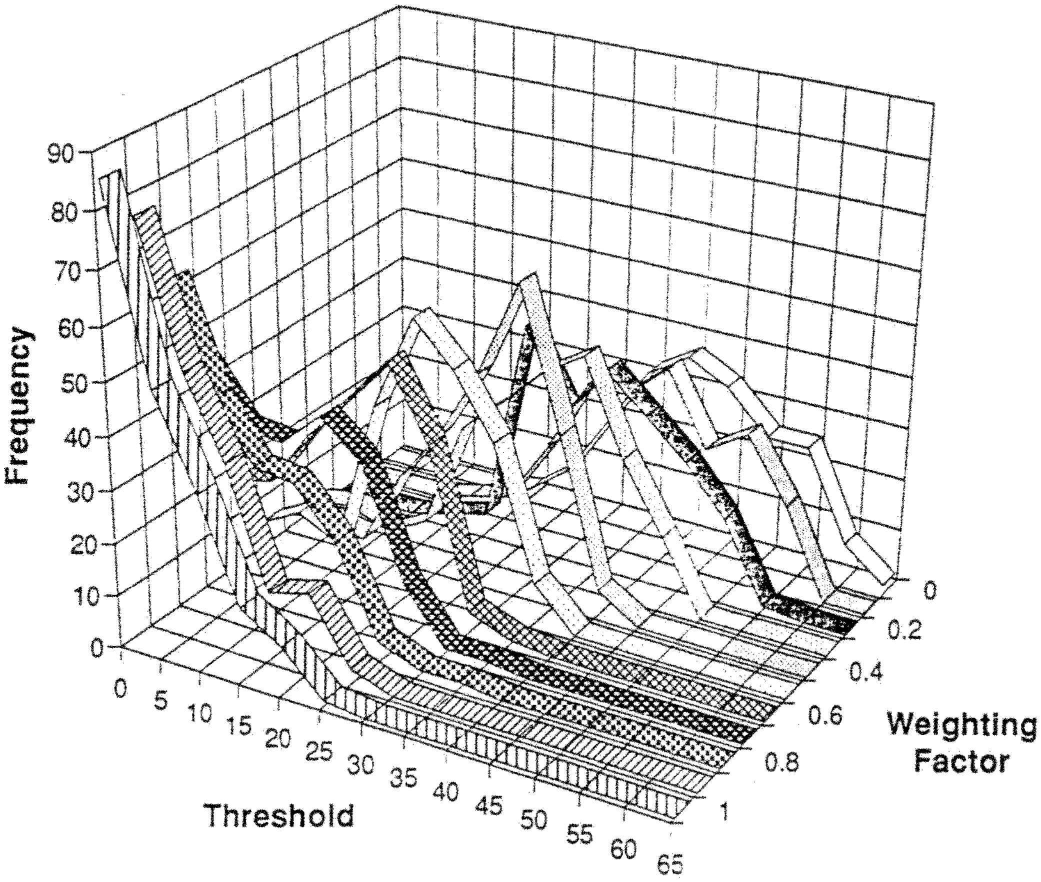

Figure 3.8. Frequency distributions of optimal threshold levels over penalty weighting factor λ of 0-1.0 from all scenarios for the first optimization problem.

of average yield and decreases of standard deviation. As λ varied from 0.5 to zero, more weight was given to average yield; as λ was changed from 0.5 to 1, heavier weight was given to standard deviation. The distribution of the optimal thresholds was the least broad with λ = 0.5. In Figure 3.8, the distribution of optimal thresholds is shown over all scenarios. The mode of this distribution shifted as a function of penalty weighting factors from high to low threshold levels: the mode being about 40-45% of the pristine biomass when average yield is the sole optimization criterion, about 20-25% for equal weighing of yield and standard deviation (λ = 0.5) and about 0% with minimum standard deviation as the criterion.

I illustrate the effects of different factors on the optimum threshold level by using a λ of 0.5. The associated percentages of gained yields, standard deviations, decreased percentage of median rebuilding time, and number of years of no fishing are given for each scenario (Table 3.3). Under scenarios with the Ricker model with medium reproductive potential, the optimal thresholds ranged from 20-30%, with a median of 25%. The increases in yield based on these threshold levels were about 17-31% for low fishing mortality, 5% initial biomass and a 20-year planning horizon; 4-9% for a 50-year planning horizon. Under high fishing mortality scenarios, these figures changed to 64-120% and 5-50%, respectively. Standard deviations increased less than the increases in yield under scenarios with low fishing mortality, but more under scenarios with high fishing mortality. There were several scenarios under which the yields increased while the standard deviations decreased. For the Ricker model with 5% initial biomass, the rebuilding times were reduced to about 25-35% for low fishing and 54-82% for high fishing. Fishing would not occur for up to 10 years under some scenarios, but in most cases there were only about 2-4 years of cessation of fishing. Percentages of increase in yield and standard deviation and percentages of decrease in rebuilding time were much smaller under scenarios with 15% initial biomass.

Optimal thresholds for scenarios with the Beverton-Holt model with 5% initial biomass were much lower than for the Ricker model and varied greatly, ranging from 0 to 30% with a median of 15% (Table 3.3). The percentages of increase in yield were much smaller than those with the Ricker model. The benefits of using the threshold management policy completely disappeared under scenarios with 15% of pristine biomass as an initial biomass.

The first-order effects of the seven different factors in determining optimal threshold levels were estimated from all 192 scenarios by constructing the frequency distributions of the optimum threshold level, amalgamating over all other factors. The results are illustrated in Figure 3.9 with λ equal to 0 (maximizing average yield), 0.2 (maximizing average logarithm of yield) and 0.5 (equal trade-off between average yield and standard deviation). Optimum threshold levels are highest for the objective function for maximum yield, because the logarithmic and equal tradeoff objective functions penalize for the higher standard deviation with higher threshold levels. A threshold level would only rarely be implemented with the minimum standard deviation policy ($\lambda = 1$, not shown), because standard deviation increases with threshold level under most scenarios.

The most important factors in determining optimal threshold level appear to be the reproductive potential and spawner-recruit model. Reproductive potential was negatively associated with the threshold levels, with high reproductive potential resulting in low threshold levels. Threshold levels for the Ricker model were much higher than those for the Beverton-Holt model.

There were some interactions of the objective function with the factors considered. When heavier weight was given to standard deviation (an increase in λ), fishing mortality had little effect on optimal threshold levels. Optimal threshold levels increased markedly as fishing mortality increased when the criterion was to maximize average yield. This is intuitive because a high threshold level can bring an overfished population back to a high productivity level quickly. Thus average yield increased, but at a cost of increasing the variation in yield. Planning horizon had little effect on optimal threshold levels, except that the optimal threshold level for the longer horizon was slightly higher for the equal trade-off function. Zero and 0.5 environmental autocorrelation had similar distributions of optimal threshold level, both slightly lower

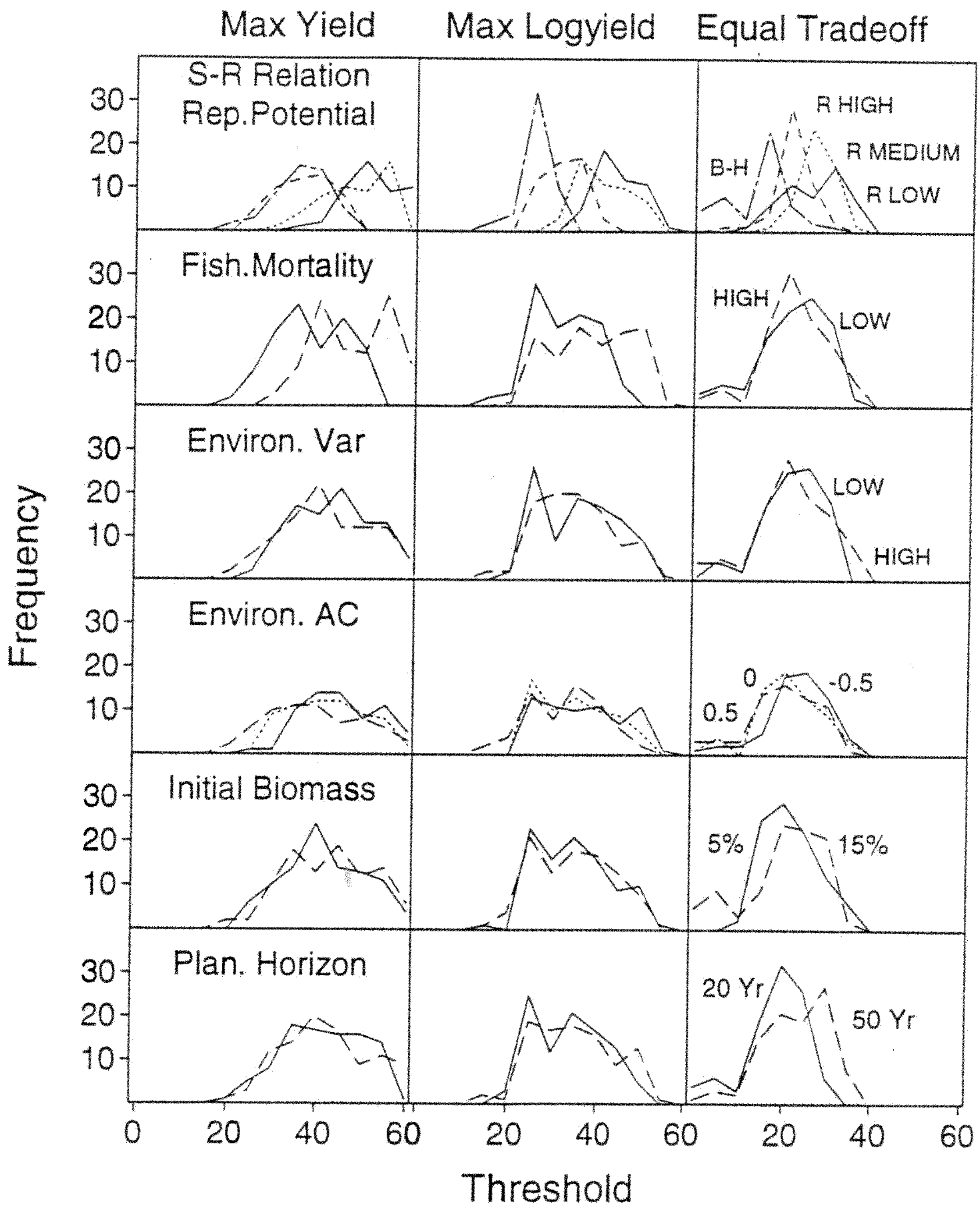

Figure 3.9. Frequency distributions of optimal threshold levels from all scenarios for the first optimization problem, classified by seven factors used in the simulation. The frequencies for each factor are amalgamated over other factors. (R: Ricker model, B-H: Beverton-Holt model).

than those with -0.5 autocorrelation. Overall, environmental autocorrelation, environmental variation, initial biomass and planning horizon had minor effects on optimal threshold levels.

Simultaneous Optimization of Threshold Level and Fishing Mortality

The above optimal threshold levels were estimated under a given level of fishing mortality. For this part of the study, the search for optimal levels was made across the two-dimensional space of threshold level and fishing mortality with a grid method. Both threshold levels ranging from 0 to 60% of pristine biomass and fishing mortalities from 0.1 to 0.85 were divided into 14 small grids. Numerical simulations were run at all grids for each combination of the factors. Only the Ricker model with the medium reproductive potential was considered in this part of the study, which corresponds to factor levels estimated for pollock from current data. The results are illustrated with three levels of penalty weighting factor λ: 0 (maximizing average yield), 0.2 (maximizing logarithm of yield) and 0.5 (equal trade-off).

A unique optimal combination of threshold level and fishing mortality existed for all scenarios. With 5% initial biomass, the optimal threshold ranged from 10 to 60% of pristine biomass, and the optimal fishing mortality was usually equal to or slightly above F_{MSY} (Table 3.4). The optimal threshold and fishing mortality declined as a function of λ, and were fairly robust to variations in the other factors. Average yield and standard deviation for the optimal levels were affected by the level of environmental variation, autocorrelation, and planning horizon, all of which influence average recruitment levels. Scenarios with 15% initial biomass produced similar qualitative conclusions. The one extreme result with an optimal F of 0.82 and an optimal threshold level of 60% may be an artifact of the simulation (Table 3.4).

To compare results under different scenarios on a common scale, I show results as contour plots of the objective function for each scenario scaled to a maximum value of 1 as a function of fishing mortality and threshold level. The absolute yields and standard deviations for the optimal combinations of threshold levels and fishing

Table 3.4. Optimal fishing mortality and threshold levels for combinations of five factors and associated levels of average yield and standard deviation. Results are given for three values of the penalty weighting factor λ: 0.0 (maximize yield), 0.2 (maximize log(yield)), and 0.5 (maximize equal tradeoff of increased yield and decreased standard deviation). Results are shown for the Ricker spawner-recruit model with medium reproductive potential.

I	E	P	AC	λ	F	T	Y	SD
5	L	20	-0.5	0	0.48	50	1.00	0.69
5	L	20	0	0	0.45	45	1.00	0.66
5	L	20	0.5	0	0.48	40	0.98	0.68
5	L	50	-0.5	0	0.82	60	1.25	1.29
5	L	50	0	0	0.48	50	1.22	0.64
5	L	50	0.5	0	0.45	45	1.21	0.65
5	H	20	-0.5	0	0.54	50	1.42	1.17
5	H	20	0	0	0.54	40	1.39	1.16
5	H	20	0.5	0	0.63	50	1.34	1.45
5	H	50	-0.5	0	0.63	55	1.71	1.30
5	H	50	0	0	0.54	40	1.68	1.21
5	H	50	0.5	0	0.63	50	1.63	1.59
5	L	20	-0.5	0.2	0.42	35	0.99	0.57
5	L	20	0	0.2	0.45	40	0.99	0.62
5	L	20	0.5	0.2	0.45	35	0.97	0.64
5	L	50	-0.5	0.2	0.45	40	1.23	0.46
5	L	50	0	0.2	0.45	40	1.22	0.51
5	L	50	0.5	0.2	0.45	35	1.20	0.57
5	H	20	-0.5	0.2	0.48	35	1.38	0.99
5	H	20	0	0.2	0.54	40	1.39	1.16
5	H	20	0.5	0.2	0.54	35	1.32	1.28
5	H	50	-0.5	0.2	0.54	45	1.70	1.08
5	H	50	0	0.2	0.54	40	1.68	1.21
5	H	50	0.5	0.2	0.54	35	1.61	1.43
5	L	20	-0.5	0.5	0.42	25	0.96	0.53
5	L	20	0	0.5	0.42	25	0.95	0.54
5	L	20	0.5	0.5	0.42	25	0.94	0.58
5	L	50	-0.5	0.5	0.42	25	1.21	0.43
5	L	50	0	0.5	0.42	25	1.20	0.47
5	L	50	0.5	0.5	0.45	30	1.19	0.55
5	H	20	-0.5	0.5	0.48	30	1.36	0.96
5	H	20	0	0.5	0.48	20	1.29	0.99
5	H	20	0.5	0.5	0.45	20	1.25	1.13
5	H	50	-0.5	0.5	0.45	20	1.64	0.95
5	H	50	0	0.5	0.48	25	1.63	1.08
5	H	50	0.5	0.5	0.39	10	1.42	1.18

Table 3.4 (continue)

I	E	P	AC	λ	F	T	Y	SD
15	L	20	-0.5	0	0.48	45	1.17	0.53
15	L	20	0	0	0.45	45	1.16	0.57
15	L	20	0.5	0	0.48	45	1.15	0.66
15	L	50	-0.5	0	0.82	60	1.31	1.30
15	L	50	0	0	0.45	45	1.29	0.48
15	L	50	0.5	0	0.48	45	1.27	0.62
15	H	20	-0.5	0	0.54	55	1.61	1.18
15	H	20	0	0	0.54	45	1.59	1.19
15	H	20	0.5	0	0.54	40	1.52	1.32
15	H	50	-0.5	0	0.54	45	1.79	1.08
15	H	50	0	0	0.54	50	1.75	1.25
15	H	50	0.5	0	0.63	45	1.71	1.55
15	L	20	-0.5	0.2	0.45	40	1.16	0.47
15	L	20	0	0.2	0.45	35	1.14	0.48
15	L	20	0.5	0.2	0.42	35	1.13	0.54
15	L	50	-0.5	0.2	0.45	40	1.29	0.36
15	L	50	0	0.2	0.45	35	1.28	0.41
15	L	50	0.5	0.2	0.45	35	1.26	0.51
15	H	20	-0.5	0.2	0.48	45	1.60	1.02
15	H	20	0	0.2	0.48	35	1.57	1.06
15	H	20	0.5	0.2	0.45	30	1.50	1.22
15	H	50	-0.5	0.2	0.54	45	1.79	1.08
15	H	50	0	0.2	0.54	40	1.75	1.15
15	H	50	0.5	0.2	0.54	35	1.68	1.40
15	L	20	-0.5	0.5	0.42	30	1.13	0.42
15	L	20	0	0.5	0.42	30	1.13	0.46
15	L	20	0.5	0.5	0.39	25	1.10	0.49
15	L	50	-0.5	0.5	0.42	30	1.28	0.34
15	L	50	0	0.5	0.42	30	1.27	0.40
15	L	50	0.5	0.5	0.42	30	1.25	0.49
15	H	20	-0.5	0.5	0.54	35	1.56	0.92
15	H	20	0	0.5	0.45	30	1.52	0.97
15	H	20	0.5	0.5	0.48	20	1.41	1.11
15	H	50	-0.5	0.5	0.54	30	1.74	0.92
15	H	50	0	0.5	0.45	35	1.70	1.04
15	H	50	0.5	0.5	0.42	25	1.60	1.26

Abbreviations:
I: initial biomass (%).
E: environmental variation: LOW (L) and HIGH (H).
P: planning horizon (yr).
AC: environmental autocorrelation.
F: fishing mortality.
T: threshold level (%).
Y: average yield.
SD: standard deviation of yield.

mortalities are given in Table 3.4. Because environmental autocorrelation had little effect on the optima, results are shown only for zero autocorrelation. Figure 3.10 illustrates results with 5% initial biomass. For the maximum yield criterion, the optimal threshold levels ranged from 40 to 50% of pristine biomass and the optimal fishing mortalities from 0.42 to 0.54 (Figure 3.10). For each scenario, there is a broad region between the 0.8 contour line and the maximum value at 1, which represents all the possible combinations of the two-parameters that would produce approximately 80% or more of the maximum yield. Such a flat response suggests that two-parameter optimization would enhance the flexibility of management, because several combinations of fishing mortalities and threshold levels would produce yields very close to the maximum yield. The threshold level commences its effect at a fishing mortality of about 0.3, which is close to $F_{0.1}$ of 0.31. For the same objective value, higher fishing mortality requires a higher threshold level. In other words, the threshold level performs the role of reducing average fishing mortality over time by fishery closure. For lower fishing mortalities (less than $F_{0.1}$), the contour lines are flat, i.e., the threshold does not have much effect. This result is a consequence of the higher equilibrium biomass for lower fishing mortality such that the population rarely fell below the threshold levels after initial rebuilding. The results appear to be robust to environmental variation, environmental autocorrelation and planning horizon, as in the one-parameter optimization. A longer planning horizon induces a slight broadening of the contour surface in a low threshold region as the benefits of the threshold wane at low fishing mortalities.

For the log(yield) criterion, the optimal threshold levels were 40% of pristine biomass, and the optimal fishing mortalities ranged from 0.45 to 0.54 for all scenarios, both being slightly lower than for the maximum yield criterion (Figure 3.10). A slight narrowing of the contours about the optimum point occurred, which reduces the combinations of the two parameters that would be close to the optimum. Other factors did not have much effect on the location of the optimum point.

For the equal trade-off criterion, the optimal threshold level varied from 20 to

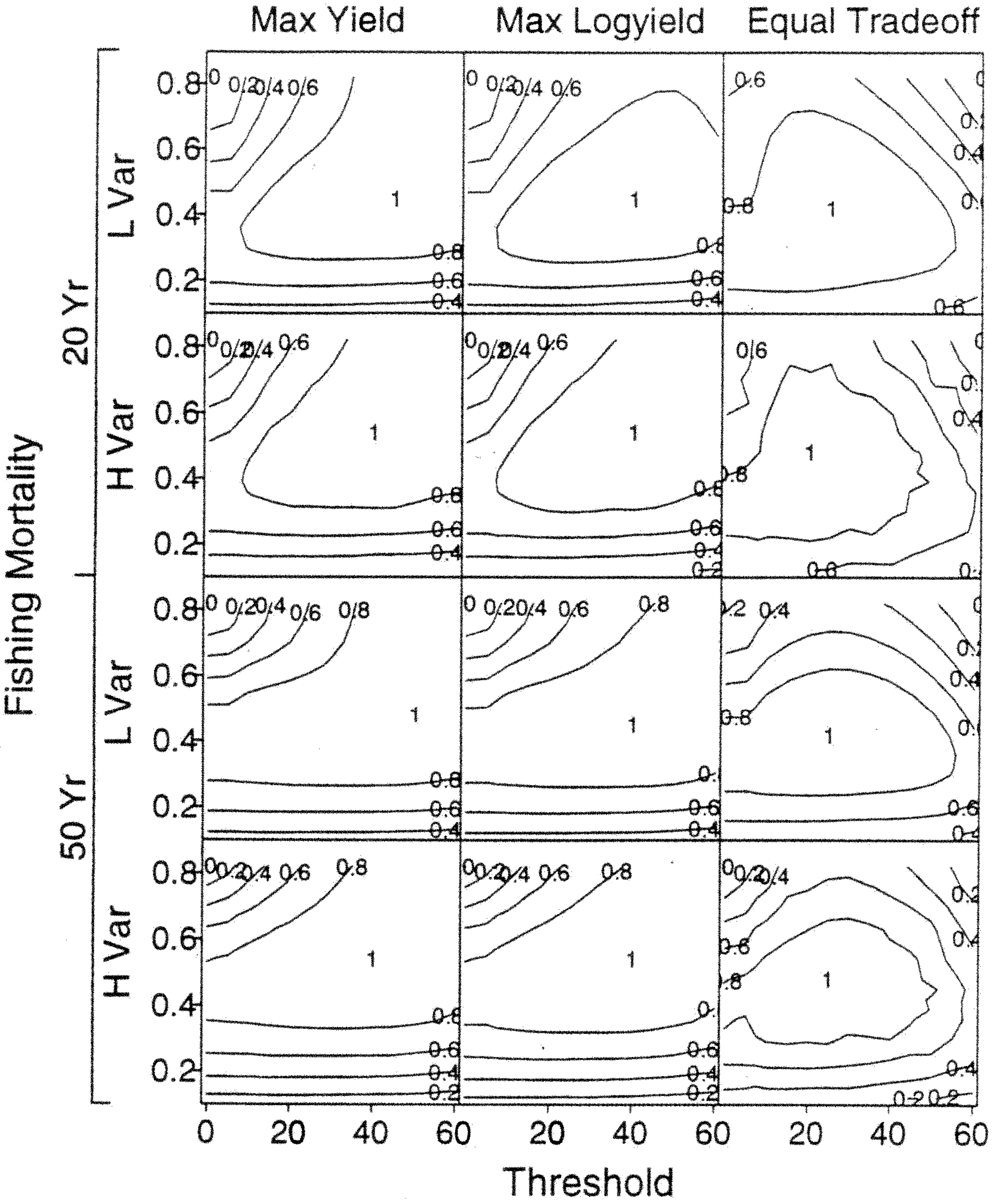

Figure 3.10. Contour plots for the second optimization problem as a function of fishing mortality and threshold level for three values of the penalty weighting factor λ (0: Max Yield, 0.2: Max Logyield, 0.5: Equal Tradeoff). The Ricker model with medium α and zero autocorrelation was used and initial biomass was 5%. The plots are also classified by environmental variation (LOW: L Var, HIGH: H Var) and planning horizon (20-yr, 50-yr). The contour values were scaled from the minimum value (0) to the maximum value (1).

25% of pristine biomass, much lower than for log(yield) criterion, and the optimal fishing mortalities ranged from 0.42 to 0.48 for all scenarios (Figure 3.10). A further narrowing of the contours about the optimum point occurred, which further reduces the combinations of the two parameters that would be close to the optimum.

Figure 3.11 illustrates the results with 15% initial biomass. The contour plots are similar with 5% initial biomass, except that the contour is broadened in the region with low threshold level. The threshold level did not have much effect for levels below 10% of pristine biomass because it was rare for the population to drop below such low threshold levels. The optimal combinations of the two parameters are very close to each other with 5% and 15% initial biomass, suggesting the initial biomass has little effect on the optimum.

DISCUSSION

Management policies that maximize average yield (maximum harvest strategies) will also tend to result in high variation in yield. Such policies usually drive the population close to the most productive level as quickly as possible and are very sensitive to environmental variation. This result can be in direct conflict with some management objectives, such as short term economic stability. The fixed escapement policy, used mainly in management of salmon populations, is a typical example of maximum harvest strategies (Reed 1979). Another common fisheries management strategy, constant harvest rate policy, as Walters (1986) noted, gives a good balance between average yield and variation in yield, provided the stock has not been and is not being driven too far from the high productivity level. Hightower and Grossman (1985), comparing the performance of different levels of constant harvest rates for fish stocks with variable recruitment, indicated that under highly variable environmental conditions, fishing effort does not affect average yield significantly, provided that fishing effort is not too far from MSY effort. Gatto and Rinaldi (1976) compared average yield and variation in yield in fluctuating environments for these two kinds of fisheries management strategies and demonstrated analytically that fixed escapement policies

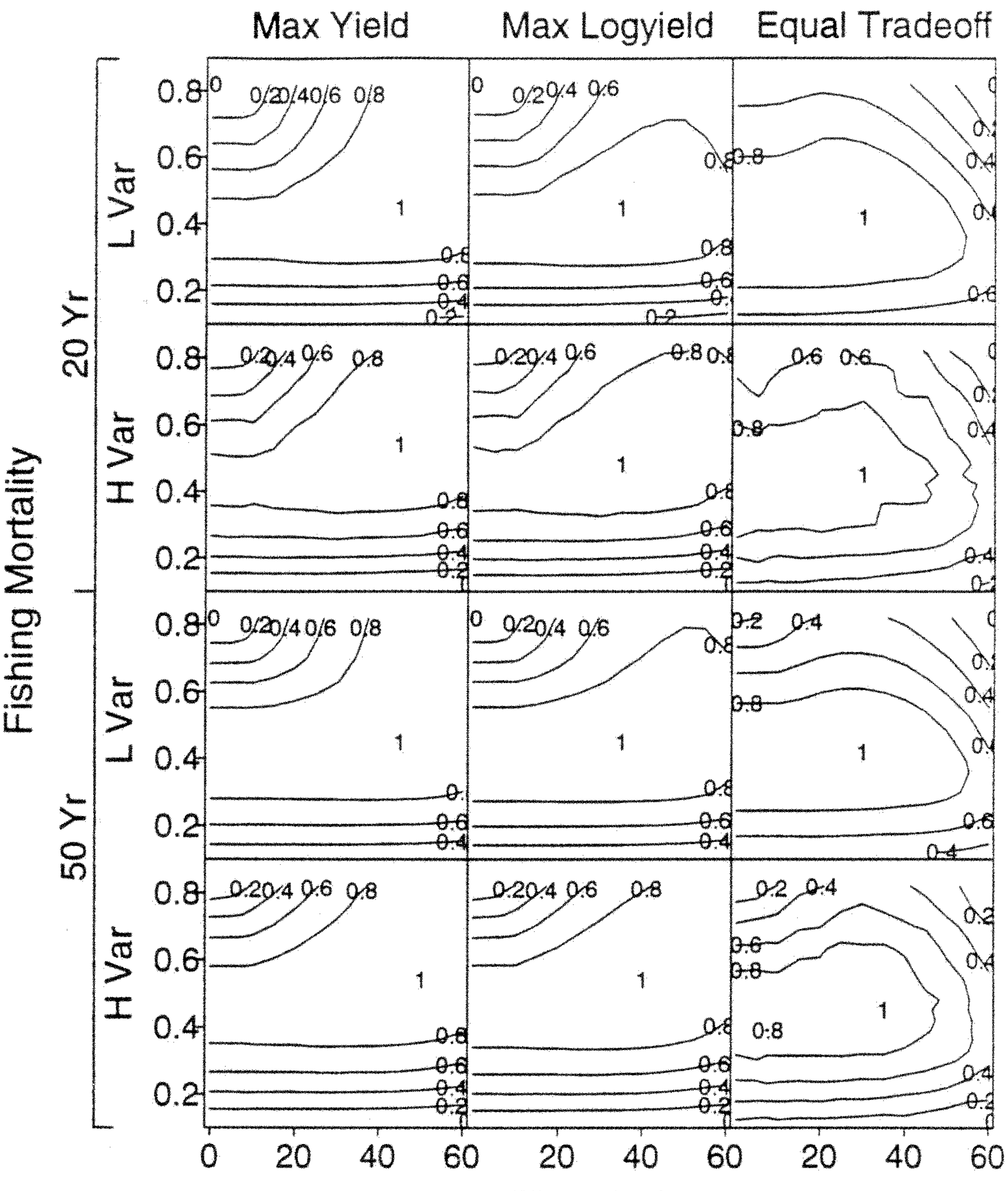

Figure 3.11. Contour plots for the second optimization problem as a function of fishing mortality and threshold level for three values of the penalty weighting factor λ (0: Max Yield, 0.2: Max Logyield, 0.5: Equal Tradeoff). The Ricker model with medium α and zero autocorrelation was used and initial biomass was 15%. The plots are also classified by environmental variation (LOW: L Var, HIGH: H Var) and planning horizon (20-yr, 50-yr). The contour values were scaled from the minimum value (0) to the maximum value (1).

should generally produce both higher average yield and higher variance in yield than constant harvest rate policies. Deriso (1985) showed that constant harvest rate policies are risk-averse.

Threshold management strategy synthesizes constant harvest rate and fixed escapement policies. It is identical with the former when the stock is at a high population level, and adapts the strategy of the latter when the population has dropped to a low level. My results show that for a simulated pollock population, management policies that set thresholds always produced some benefits in increased yield, even when variation in yield also increased, and can, in some cases, increase average yield greatly while increasing variation in yield only slightly over the entire period and over the first 20 years of the experiment. Environmental variation, environmental autocorrelation and initial biomass had relatively little effect on my conclusions.

Optimal threshold levels for EBS pollock range from 5% to 60% of the pristine biomass, depending upon the trade-off between the increase of yield and the decrease of variation in yield. A compromise trade-off giving equal weight to these two components results in the most robust optimal threshold levels, in the 20%-30% range of values with a median of 25%, for the Ricker spawner-recruitment model with the medium reproductive potential. These optimal threshold levels are slightly higher than the 20% level proposed by Thompson (*in press*). Optimal fishing mortality rates are equal to F_{MSY} or slightly higher. The response surfaces are flat with two-parameter optimization, which provides flexibility for management. These results were relatively independent of the effects of environmental variation, environmental autocorrelation, planning horizon and initial biomass. However, their possible robustness in a multi-species context is not known.

Threshold management policies may be close to optimal regarding the class of all possible policies for single-species models. In a study of an age-structured population, Hightower and Grossman (1987) used a first-order gradient procedure to obtain optimal strategies under several maximized criteria. Frequently, their results showed that the optimal strategy was no fishing for a few years followed by a fairly constant fishing effort. In a study of optimal harvesting policies for the widow rockfish fishery, Hightower and Lenarz (1989) investigated several policies and concluded that a two-parameter policy, such as constant fishing mortality with a threshold, may not necessarily be more beneficial than a one-parameter policy of constant fishing mortality. In contrast, my study showed that the use of a threshold produces distinct benefits. This suggests that optimal policies may be somewhat dependent on the species considered, or the conditions simulated.

An alternative to the trade-off model between average yield and variation in yield (equation 3.7) for selecting a desirable threshold is the Pareto Frontier (Walters 1975), where average yield is plotted against standard deviation of yield over different threshold levels. It gives a visual display of combinations of yield and variation in yield, but scale problems occur when comparing the effects of different factors.

The simulations showed that the spawner-recruitment relationship and reproductive potential had significant effects on optimal threshold levels, which suggests that there may exist other biological reference points more robust than the one expressed as a percentage of pristine biomass, or optimal threshold levels may be a function of several population parameters. I will investigate alternative methods to estimate threshold levels in chapter five.

In this part of my study, for simplicity I assumed that we could measure the population and implement the harvest strategies perfectly. In reality, there exist errors in measuring the population and implementing the harvest strategies. I will examine the effects of these errors on optimal threshold levels in Chapters 5 and 6.

The threshold assumed for pollock was based on single-species considerations and did not consider interactions with other marine species, including marine mammals and seabirds. Certain marine mammals and seabirds feed on pollock and there has been much recent discussion of possible impacts of pollock population fluctuations on them in Alaska (Springer and Byrd 1989; Lowry et al. 1989). If species interactions can be included in future experiments with threshold models, we will learn the probable impact of these policies on pollock as well as other Bering Sea species. Furthermore, density-dependent effects on post-recruit natural mortality due to cannibalism and other intraspecies effects could be important as well. I will conduct sensitivity analyses of density-dependent natural mortality on optimal threshold levels for EBS herring in Chapter six.

An alternative approach to threshold management strategies is biomass-based strategies. Under biomass-based strategies, the fishing mortality is equal to F_{MSY} when the population biomass is equal to or above B_{MSY}; the fishing mortality varies linearly with the population biomass from zero to F_{MSY} when the population increases from zero to B_{MSY} (NPFMC 1991). In recent years, the plan team for the groundfish fisheries of the Bering Sea and Aleutian Islands has used biomass-based strategies to compute the maximum allowable biological catch for EBS pollock (NPFMC 1991). Biomass-based strategies do not stop fishing completely and thus produce relatively short-term economic stability. Biomass-based strategies are attractive for fisheries like EBS pollock, in which alternative resources are not available and bycatch problems are an important concern. But biomass-based strategies may not have the same level of resource protection as threshold strategies when the population is at a low level and it may be difficult to allocate catch quota among users when the quota is small.

Chapter Four

EVALUATION OF THRESHOLD MANAGEMENT STRATEGIES FOR PACIFIC HERRING IN ALASKA

SUMMARY

Computer simulations were conducted to evaluate threshold management strategies for herring stocks in the eastern Bering Sea (EBS) and Prince William Sound (PWS), Alaska, based on a single-species model. Population parameters were derived from cohort analysis, catch-at-age analysis, and catch and population sampling. Several threshold values ranging from 0 (no threshold) to the biomass level producing MSY, in combination with different exploitation rates from 5% to 60%, were examined. Other factors investigated were recruitment, initial biomass, natural mortality, implementation error, and measurement error. Three criteria used to evaluate the threshold management strategies were the trade-off between mean yield and standard deviation of yield, harvest opportunity, and variation of spawning biomass. Recruitment, especially stock-recruitment relationships, and exploitation rate are the most important factors influencing optimal threshold levels. The combination of a high threshold level and a high exploitation rate approximates a pulse fishing scenario that results in the highest yield and variation in yield. Large measurement error decreases both the optimal exploitation rate and threshold level. For EBS herring, optimal thresholds range from 10% to 25%, median of 20%, of pristine biomass under an exploitation rate of 20% ([2]$H_{\text{status quo}}$) and from 10% to 35%, median of 30%, of pristine biomass under an exploitation rate of 31% ($H_{0.1}$). Optimal thresholds for PWS herring vary from 5% to 25%, median of 15%, of pristine biomass and from 0 to 45%, median of 25%, with

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[2] $H_{\text{status quo}}$ is the exploitation rate currently used to manage the fishery. $H_{0.1}$ is the exploitation rate at which the slope of the yield per recruit curve as a function of exploitation rate is equal to 10% of its value at the origin. H_{MSY} is the exploitation rate at which MSY is achieved.

exploitation rates of $H_{status\ quo}$ and $H_{0.1}$, respectively. Rebuilding time with a threshold approach is much shorter than with an exploitation rate approach alone.

INTRODUCTION

Pacific herring, *Clupea pallasi*, sustain one of the most important fisheries in the State of Alaska. Commercial exploitation of herring in Alaska started at the beginning of the 20th century, with two peak harvests of about 150,000 tonnes in 1934 and 1969 (Funk and Harris 1992). Herring were harvested primarily by a reduction fishery for oil and meal products before 1960 (Funk and Harris 1992). Trawl fisheries of herring in the EBS were developed by the Soviet Union and Japan in 1959 and were phased out in the early 1980's (Wespestad 1991). Sac roe fisheries began in the early 1970's and have become important statewide fisheries, occurring from Kah Shakes in Southeast to Port Clarence in the north (near the Arctic area). The largest herring fisheries are currently located in Togiak, Prince William Sound, Cook Inlet, Kodiak, Sitka Sound and Norton Sound (Funk and Harris 1992).

This study focussed on PWS and EBS herring stocks. In PWS, Alaska Board of Fisheries regulations distribute the allowable harvest among five fisheries: sac roe purse seine (58.1%), sac roe gillnet (3.4%), pound spawn-on-kelp (14.2%), natural spawn-on-kelp (8%), and food/bait (16.3%). In the southeastern Bering Sea, primarily the Togiak area, the regulations set aside 1361 tonnes of the allowable catch for the natural spawn on kelp fishery, 7% of the remaining allowable catch to the food/bait fishery, and the remainder to the sac roe fishery, of which 75% is allocated to the purse seine fleet and 25% to the gillnet fleet. In the central and northern EBS, primarily Norton Sound area, more than 90% of the allowable catch is allocated to the sac roe gillnet fishery and the balance to the sac roe beach seine fishery.

For the purpose of management, PWS herring are assumed to be a single stock. Although Sandone et al. (1988) reported that length-at-age of herring from the food/bait fishery in the fall in southeastern PWS during some years was significantly different from that in the spring sac roe fisheries, Burkey (1986) found no genetic and scale pattern differences among herring spawning at different locations inside PWS. PWS herring are geographically separated from other spawning stocks.

Based on the geographic separation of spawning grounds, there are more than a half dozen herring stocks in the EBS. However, only three distinct stocks are apparent in growth data: a southern stock which spawns at Togiak, Security Cove, and Goodnews Bay; a central stock which spawns between the mouths of the Kuskokwim and Yukon rivers; and a northern stock which spawns at Norton Sound and Port Clarence (Wespestad 1991). Despite spawning, geographic and growth differences, no significant genetic differences among the stocks from Norton Sound to Togiak have been found (Grant and Utter 1984). For purposes of this analysis, I regard all EBS herring as one single stock. This simplification allows me to make maximum use of existing data. Furthermore, this simplification is pragmatic: about 80% of herring in the EBS spawn in one location, Togiak (Wespestad 1991).

Herring fisheries in Alaska have followed a boom-and-bust syndrome typifying herring fisheries throughout the world. Catches have ranged from under 10,000 tonnes to over 150,000 tonnes during the past six decades. Variations in herring populations are caused by both environmental factors and human exploitation (Wespestad 1991). To prevent overfishing, the goals of Alaska herring fisheries management are to protect the sustained yield of the stocks and to provide an equitable distribution of the available harvest between various users (ADF&G 1992). In an attempt to stabilize the fisheries, Alaska herring fisheries have been managed with a range of perceived conservative exploitation rates of 0-20% since the early 1970's. In recent years, thresholds have been established to be 20% or 25% of the "normal" biomass level. Methods to establish this normal biomass level vary among areas. The effectiveness of the overall herring harvest strategy has never been explicitly analyzed.

The purpose of this study (based on Zheng et al. *in press* a) was to evaluate and compare the current management strategy with alternative threshold management strategies through computer simulations for PWS and EBS herring stocks. The threshold management strategy is defined such that harvesting occurs at a constant exploitation rate but ceases when a population drops below a threshold level (Quinn et al. 1990). A threshold is defined as a percentage of pristine biomass which is estimated as a long-term average of biomass in the absence of fishing and under average environmental conditions. In this chapter, age-structured models were constructed to analyze the population dynamics of EBS and PWS herring stocks under various thresholds. The effects of some important factors--recruitment, initial biomass, natural mortality, and error--on each threshold management strategy were investigated. Optimal threshold and exploitation rate levels were estimated as a function of average yield and standard deviation of yield.

METHODS

Data Analysis

Natural mortality, maturity and catch-age data of EBS herring from 1959 to 1988 were provided by Wespestad (1991), and the catch-age data were updated with the recent data from Alaska Department of Fish and Game. Mature population abundances, weight and age compositions estimated from aerial surveys and test (experimental) fishing were available for EBS herring after 1977. Table 4.1 summarizes the population parameters.

Wespestad (1991) applied cohort analysis to EBS herring. In his cohort analysis, catch data were truncated at age 9, and for each year from 1959 to 1977 the averages of fishing mortalities over ages 7 and 8 were used as terminal fishing mortalities at age 9. Terminal fishing mortalities after 1977 were tuned using the test fishing age composition data in 1978, 1982, 1984, and 1988; population abundance was assumed to equal aerial survey abundance in the terminal year (1988). Because the aerial survey abundances are considered unreliable (Baker 1991; Wespestad 1991), cohort analysis tuned with only one source of auxiliary information (age compositions of spawning population) is a natural choice for stock-reconstruction of EBS herring.

To update the cohort analysis, I followed, with some modifications, Wespestad's approach. In my cohort analysis, I used the same natural mortalities as those used by

Table 4.1. Estimates of natural mortality, maturity, selectivity, and growth and stock-recruit parameters of eastern Bering Sea (EBS) and Prince William Sound (PWS) herring.

Age	Natural mortality		Maturity		Selectivity				
	EBS	PWS	EBS	PWS	EBS	PWS			
					SR	SRPS	SRGN	Pound	F/B
3	0.25	0.43	0.40	0.20	0.05	0.09	2e-4	0.20	0.71
4	0.15	0.43	0.83	0.68	0.14	0.40	0.02	0.53	1.00
5	0.18	0.43	0.96	0.95	0.31	0.91	0.20	0.80	0.80
6	0.23	0.43	1.00	0.99	0.39	0.99	0.60	0.99	0.50
7	0.29	0.43	1.00	1.00	0.70	1.00	0.96	1.00	0.28
8	0.36	0.43	1.00	1.00	0.75	1.00	1.00	1.00	0.14
9	0.45	0.43	1.00	1.00	0.81	1.00	0.96	1.00	0.07
10	0.57	0.43	1.00	1.00	0.86	1.00	0.60	1.00	0.07
11	0.71	0.43	1.00	1.00	0.85	1.00	0.20	1.00	0.07
12	0.89	0.43	1.00	1.00	1.00	1.00	0.02	1.00	0.07
13	1.12	0.43	1.00	1.00	1.00	1.00	2e-4	1.00	0.07

Growth (kg) Parameters	EBS	PWS	
	Spawning	Spawning	F/B
W_∞ =	0.5618	0.2036	0.1158
k =	0.2000	0.2856	0.4472
t_0 =	-1.8530	-1.450	-1.771
b =	3.4044	3.283	2.890

Stock-recruit Parameters	EBS	PWS		
		No-cycle	Cycle	
α =	6.7028	12.039	15.278	42.478
β =	0.0054	0.0215	0.037	0.0145
σ =	1.0000	1.2900	0.800	0.6
SD(α) =	2.3770	8.7564	7.6936	NA
SD(β) =	0.0010	0.0127	0.0094	NA
R^2 =	0.54	0.15	0.56	NA
DF =	24	16	12	3

Abbreviations:
SR: sac roe
SRPS: sac roe purse seine
SRGN: sac roe gillnet
Pound: pound spawn-on-kelp
F/B: food/bait.

Wespestad (1991). However, the catch data were truncated at age 12, and terminal fishing mortalities at age 12 for each year from 1959 to 1977 were set equal to the averages of fishing mortalities from ages 7 to 11. This assumed the same catchability for these age groups. Furthermore, the terminal fishing mortalities after 1977 were adjusted using the age composition data from test fishing in 1978 and from 1982 to 1990. Adjustments were made until the estimated population had the closest age composition to those of test fishing. The important difference between the results of my cohort analysis and those of Wespestad (1991) was that I estimated the peak biomasses in the 1960's and 1980's to be of similar magnitude, whereas Wespestad (1991) estimated the peak biomass in the 1960's to be about twice as large as that in the 1980's.

A variety of data sources are available for PWS herring (Funk and Zheng 1992a). Catch-age data were classified by fishery and gear type from 1973 to 1992. Mature population abundances and age compositions were estimated by aerial surveys in 1974, and from 1976 to 1991, and spawning abundances by age were estimated through spawn deposition surveys for six years: 1984 and 1988-1992. In addition, the number of miles of milt observed by the aerial surveys from 1972 to 1992 was used as a relative index of abundance.

To take advantage of the auxiliary information, catch-age analysis with auxiliary information (Deriso et al. 1989) was applied to PWS herring. Funk and Sandone (1990) conducted the initial catch-age analysis which was updated by Funk and Zheng (1992a). Natural mortality, maturity, and selectivities were estimated from the catch-age analysis and summarized in Table 4.1. The results of the updated catch-age analysis were used in this study.

Since 1959, three very strong year-classes (1962, 1977, and 1978) of EBS herring have occurred (Figure 4.1; Chapter 2). Environmental variation was assumed to be the cause. Recruitment appears to decline asymptotically with extremely large spawning biomass, suggesting the Ricker curve as a good candidate for the stock-recruit model (Figure 4.1; Chapter 2). The three most recent estimates of recruits (year-classes

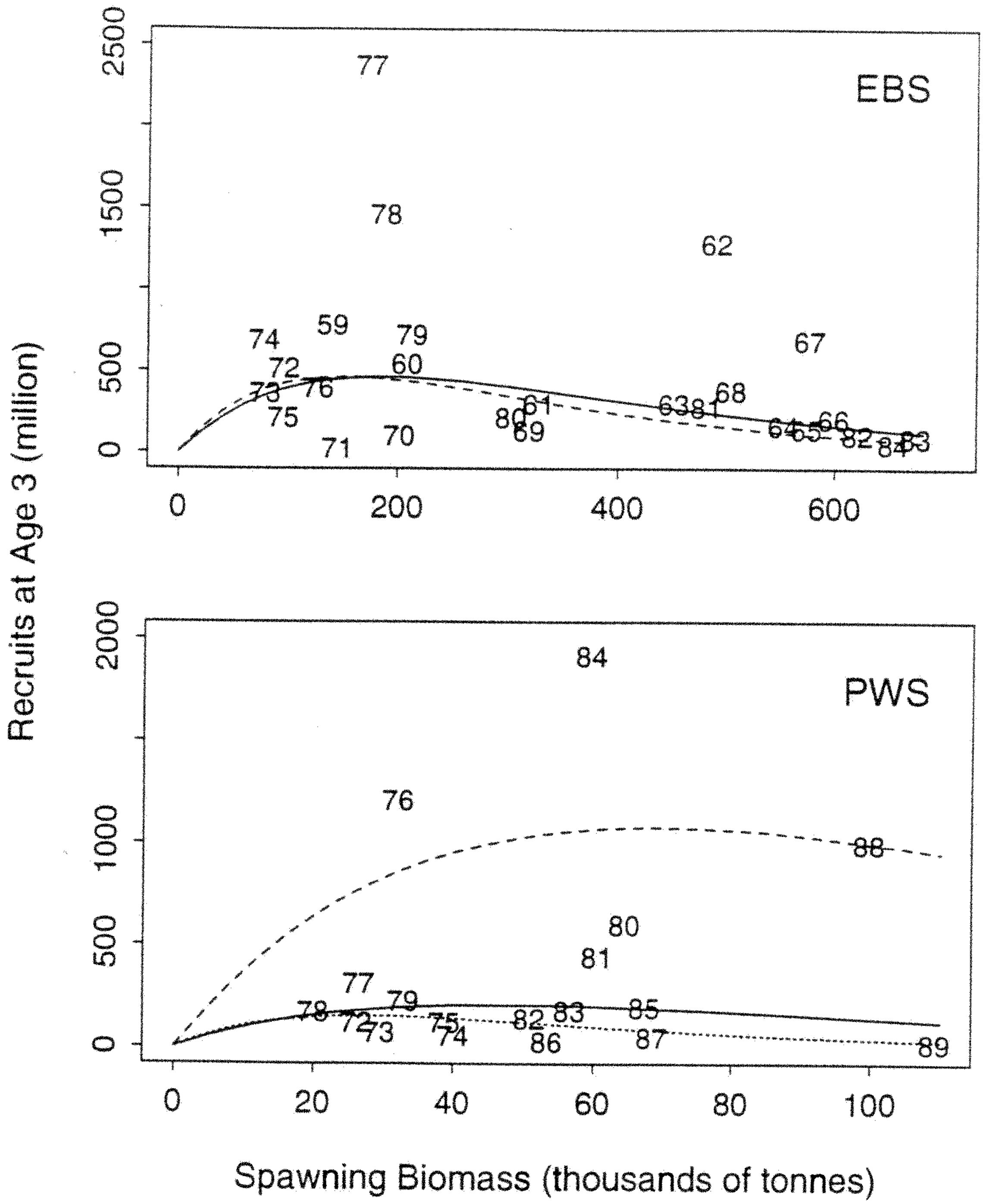

Figure 4.1. Stock-recruit estimates for each year-class and fits of Ricker models for eastern Bering Sea (EBS) and Prince William Sound (PWS) herring. For EBS data, the solid line was associated with estimated natural mortality and the dashed line with natural mortality of 0.2. For PWS herring, the solid line was fitted to all data (no-cycle), the dotted line to weak recruitment, and the dashed line to strong recruitment. The numbers in the plots are brood-year.

1985, 1986, and 1987) were highly affected by the terminal fishing mortalities and excluded from fitting stock-recruit models. I examined the sensitivity of choices of natural mortality in the cohort analysis on the shape of the stock-recruit model using constant natural mortalities ranging from 0.2 to 0.4 to repeat the cohort analysis. The stock-recruit data with different natural mortalities were standardized by a common scale and fitted to the Ricker model; the two most different curves are illustrated in Figure 4.1. The shape of the stock-recruit curve influences optimal threshold levels (Quinn et al. 1990), but the choice of natural mortalities in the cohort analysis has little effect on the shape.

Strong year-classes of herring have occurred in PWS every 4 years since 1976 (Figure 4.1). This 4-year cycle was found in other herring stocks in the Gulf of Alaska as well (Collie 1991a; Haist and Schweigert 1990; Chapter 2). This phenomenon may be caused by large-scale environmental factors, but causative factors are unknown (Chapter 2). These PWS data were interpreted in two different ways.

First, the deviations of recruits from the stock-recruit relationship were considered to be caused solely by the variation of environmental conditions. A Ricker curve was fitted to the data regardless of the known 4-year cycle (called "no-cycle"). Note that the recruits were so variable that the fitted curve explained only a very small portion of the variation. Secondly, I assumed that there may be two kinds of environmental conditions for herring recruits: every 4 years, favorable environmental conditions occurred but the environmental conditions were unfavorable otherwise. Two Ricker curves were fitted corresponding to these two environmental conditions (called "cycle"). One was fit to all data except the four strongest year-classes. The other was fit only to the four strongest year-classes. It was assumed that the stock-recruit curve shifted from the weak recruit model to the strong recruit model once every four years due to a shift to favorable environmental conditions. The initial phase of the cycle was determined randomly. Both sets of the stock-recruit models derived by these two interpretations were used in the simulation study described below.

Age-structured Model

The simulation models were similar in approach for these two herring stocks except that a different number of fisheries was modelled for each stock. To simulate herring fisheries in a realistic fashion, I modelled five herring fisheries in PWS: sac roe purse seine, sac roe gillnet, pound spawn-on-kelp, natural spawn-on-kelp, and food/bait, according to the order of their occurrence. In the EBS, I did not explicitly model the relatively small harvests by the Dutch Harbor food/bait fishery and the trawl bycatch in which exploitation rates are typically 0.5% or 1%. Because gear selectivities of purse seines and gillnets could not be separated in the cohort analysis for EBS herring, only one fishery was modelled for this population, namely the sac roe fishery. The following models were applied to PWS herring. For EBS herring, the models were identical except that the models for pound spawn-on-kelp, natural spawn-on-kelp, and food/bait fisheries were not applied.

In the spring each year before spawning, the mature herring biomass B_t was obtained as

(4.1) $B_t = \Sigma_a[N_{t,a} \quad m_a \quad w_a]$,

where $N_{t,a}$ is abundance just before spawning in year t and age a, m_a is the proportion mature and w_a is weight at age a, which is determined by a general von Bertalanffy growth equation

(4.2) $w_a = W_\infty (1 - \exp[-k(a-t_o)])^b$,

where W_∞, k, t_o and b are growth parameters.

Total yield Y_t was determined as

(4.3) $Y_t = B_t h_t$,

where h_t is exploitation rate in year t. The total yield was allocated to different fisheries by predetermined proportions p_f. To convert the yield by fishery to catch in number by age, I estimated exploitable biomass by fishery, $EB_{t,f}$,

(4.4) $EB_{t,f} = \Sigma_a[N_{t,a} s_{a,f} w_a]$,

where age and fishery selectivity coefficient $s_{a,f}$ is equal to 1 for at least one age. The effective exploitation rate by age and fishery is

(4.5) $H_{t,a,f} = p_f\, h_t\, s_{a,f}\, B_t/EB_{t,f}$.

The catches (in number) for the four spring fisheries were calculated as

(4.6) $C_{t,a,f} = N_{t,a}\, H_{t,a,f}$.

Total spawning biomass, S_t, was

(4.7) $S_t = \Sigma_a[(N_{t,a} - \Sigma_f C_{t,a,f})\, w_a\, m_a]$.

Herring caught for the pound spawn-on-kelp fishery were released after spawning and were assumed to have a 50% mortality rate (Lloyd A. Webb, Canada Department of Fisheries and Oceans, Vancouver, personal communications). Total number of fish dying due to fishing, $D_{t,a}$, was estimated as

(4.8) $D_{t,a} = C_{t,a,s} + C_{t,a,g} + 0.5\, C_{t,a,k}$,

where *s* stands for sac roe purse seine, *g* for sac roe gillnet, and *k* for pound spawn-on-kelp.

About a half year after the spring fisheries, the abundance just before the fall food/bait fishery was

(4.9) $N_{t+0.5,a+0.5} = (N_{t,a} - D_{t,a})\exp(-0.5\, M_a)$.

Catch for the food/bait fishery was obtained by multiplying the abundance with the effective exploitation rate, $H_{t,a,b}$:

(4.10) $C_{t,a,b} = N_{t+0.5,a+0.5}\, H_{t,a,b}$.

The abundance was advanced to the next year, $N_{t+1,a+1}$, as

(4.11) $N_{t+1,a+1} = (N_{t+0.5,a+0.5} - C_{t,a,b})\exp(-0.5\, M_a)$

for all ages except the oldest age in the model and by

(4.12) $N_{t+1,la} = (N_{t+0.5,la-0.5} - C_{t,la-1,b})\exp(-0.5\, M_{la-1}) + (N_{t+0.5,la} - C_{t,la,b})\exp(-0.5\, M_{la})$

for the last age (*la*) in the model. The last age is a plus group for fish older than *la*.

The Ricker model was used to describe the stock-recruit relation because of simplicity and best fit of the data:

(4.13) $N_{t+r,r} = \alpha\, S_t \exp(-\beta\, S_t + v_t)$,

where r is the starting age, α and β are parameters, and v_t is a random variable assumed to follow a normal distribution with mean 0 and variance σ^2 (Quinn et al. 1990).

Simulations

To investigate how a herring population might respond to different threshold levels and exploitation rates when fish biomass declines to low levels, I used the age-structured model for computer experiments. For this I varied threshold level, exploitation rate, and several factors influencing herring population dynamics. Threshold levels from 0 (no threshold) to 60% of the pristine biomass and exploitation rates from 5% to 60% were examined. Two different levels of initial biomass equal to 5% and 25% of pristine biomass, along with corresponding equilibrium age compositions, were assumed. Previous simulation studies on EBS pollock indicated that the effects of planning horizon on the optimal threshold levels were minor when the planning horizon was 20 years or longer (Quinn et al. 1990). Therefore, I used a fixed planning horizon of 50 years and replicated each scenario 200 times. To compare different scenarios under the same environmental conditions, I used the same set of seeds for random number generators for all scenarios. Note that 200 replicates are much smaller than 2000 or 5000 replicates used for pollock simulations in Chapter 3. Because different seeds for random number generators were used for each scenario for pollock simulations, a high number of replicates was required for meaningful comparisons.

Catches depend on exploitation rates and stock abundances which are estimated with measurement error (ME). Measurement error during stock assessments was assumed to follow a lognormal distribution. The true mature biomass B_t and exploitable biomass $EB_{t,f}$ computed in equations (4.1) and (4.4) were multiplied by the measurement error each year to obtain the estimated values. Catches also depend on how well a harvest strategy is implemented. Implementation error, defined as the difference between the intended catch quota and the actual catch, was assumed to follow a normal distribution. Thus, the actual catch each year was equal to the intended catch quota computed in equation (4.6) plus the implementation error. Three levels of measurement error and implementation error, corresponding to standard deviations of 0, 0.2, and 0.5, were examined. To prevent extremely large errors in both ends of the error distributions, I truncated the measurement errors by their 95% confidence limits and the implementation errors by their 90% confidence limits.

Consecutive poor recruitment for a number of years in conjunction with high exploitation rates is often the cause of fishery collapse. This feature was simulated by generating first-order autocorrelated errors (v_t). Two levels of autocorrelation (AC), with coefficients 0 and 0.5, were used in the simulations.

From each simulation, diagnostic statistics were (1) average yield, (2) standard deviation of yield, (3) total time below a threshold level (no fishing), (4) coefficient of variation of spawning biomass. These statistics were used as measures of the performance of harvest policy combinations of thresholds and exploitation rates. In addition, rebuilding time and total time to rebuild the population to a threshold level for the simulations with 5% initial biomass were collected to examine how a threshold level and exploitation rate would affect the time to enhance a population once it fell to a very low level.

Optimal Criteria

Management of a fishery should ideally achieve a stable optimal spawning biomass, result in a large yield, avoid large annual variation in yield, and maintain continuous harvest opportunity. Simulation results indicated that the standard deviation of yield could be used linearly to approximate the coefficient of variation (CV) of spawning biomass and the probability of no fishing. The optimization problem is then simplified because the objective function needs only to consider average yield and standard deviation of yield. I chose an objective function to provide the trade-off between increased average yield and decreased variation in yield. Detailed descriptions of this objective function are given by Quinn et al. (1990). The function is a linear combination of average yield and the standard deviation of yield over the planning horizon, or

$$(4.14) \qquad \max\ [(1 - \lambda)\ Y_{th} - \lambda\ SD_{th}],$$

where Y_{th} and SD_{th} are average annual yield and standard deviation under threshold level "*th*", and λ is a penalty weighting factor. There are three special cases: maximum average yield (λ=0), equal trade-off of increased average yield with decreased standard deviation (λ=0.5), and minimum variation in yield (λ=1.0).

Two optimization problems were considered. First, for a given exploitation rate, the optimal thresholds were found from the objective function. Second, optimal combinations of thresholds and exploitation rates were determined simultaneously using the objective function. Solution of the first optimality problem provides advice on adjustments to the current threshold level while continuing to implement the current exploitation rate policy. Solution of the second problem provides advice on the current management practices with respect to optimal threshold harvest policy.

RESULTS

Non-threshold, age-structured models with stochastic variation in recruitment for PWS and EBS herring were replicated 500 times. Each replicate was iterated for 300 years, and the results in the last 100 years were used to determine associated average mature biomass, and yield as a function of exploitation rate (Figure 4.2). For each exploitation rate, the scaled frequency distributions of mature biomass and yield are illustrated. Simulated herring population abundance and yield are extremely variable (Figure 4.2). EBS herring are about five times as abundant as PWS herring. For EBS herring, the maximum yield was achieved with an exploitation rate of 0.36 (Table 4.2), and the probability of population collapse increased dramatically with exploitation rates higher than 0.5 (Figure 4.2). For PWS herring without a 4-year cycle, exploitation rate corresponding to maximum yield (H_{MSY}) was 0.34 (Table 4.2), and an exploitation rate of 0.4 or higher result in high probability of population collapse (Figure 4.2). If strong recruitment occurred every 4 years for PWS herring, H_{MSY} was 0.42 and the population was more productive (Table 4.2).

Simulations under different threshold levels were then made for different scenarios for each herring stock. In all scenarios under a constant exploitation rate of 0.2 or higher, the average yield increased as a function of the threshold to a maximum value and then decreased. The standard deviation generally increased monotonically.

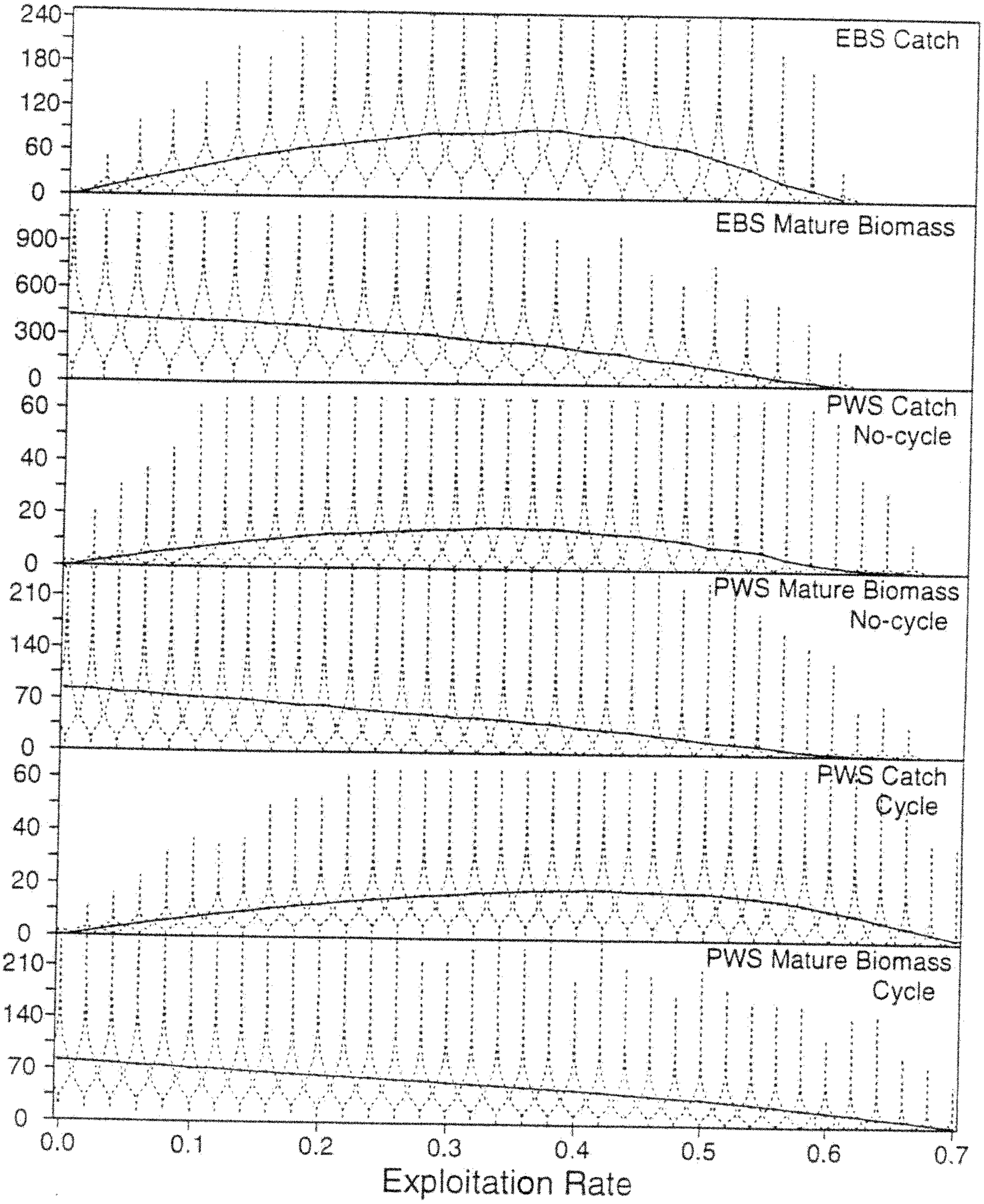

Figure 4.2. Catch and mature biomass distribution as a function of exploitation rate by computer simulations for eastern Bering Sea (EBS) and Prince William Sound (PWS) herring. The vertical dashed bars show the frequency distributions of catch and mature biomass for a given exploitation rate. The solid lines are the average catch or mature biomass. (unit: 1000 tonnes)

Table 4.2. Pristine mature biomass, mature biomass B_{MSY} at maximum average sustainable yield (MSY) and its percentage of pristine mature biomass, MSY, in thousands of tonnes, and exploitation rate H_{MSY}, for EBS and PWS herring.

	EBS	PWS	
Parameter		No-cycle	Cycle
B_∞	421.0	83.4	81.5
B_{MSY}	254.0	45.6	45.0
B_{MSY}/B_∞	0.6	0.55	0.55
MSY	92.0	15.5	18.9
H_{MSY}	0.36	0.34	0.42
$H_{0.1}$	0.31	0.40	0.40

The coefficient of variation (CV) of spawning biomass decreased with increasing threshold levels, and the proportion of years without fishing increased. The proportion of years without fishing was almost parallel to the standard deviation of yield as a function of the threshold, whereas the decreased CV of spawning biomass and the increased standard deviation of yield were roughly symmetrical over the increased threshold levels.

Figure 4.3 illustrates the benefits--increased average yield and reduced CV of spawning biomass--of introducing a threshold level for EBS herring given an exploitation rate of H_{MSY}. Measurement error generally reduced the average yield and increased the standard deviation of yield, CV of spawning biomass and proportion of years without fishing. Implementation error (not shown here) also reduced the average yield and increased the variation in yield, but the trends with threshold levels were the same under different levels of implementation errors. Environmental autocorrelation had effects similar to measurement error, but the increase in average yield with a threshold level under positive autocorrelation was slightly higher than without autocorrelation. A threshold strategy was not as beneficial when the initial biomass was high as when the initial biomass was low, because the population was less likely to drop to a threshold level when it began high. However trends with threshold levels were similar.

Simulation results for PWS herring were qualitatively similar to those for EBS herring in regard to the level of the threshold (Figure 4.4). The variation in yield and CV of spawning biomass were much larger with no-cycle of recruitment than those with a 4-year cycle, while the average yield with a 4-year cycle of recruitment was higher than with no-cycle. The strong 4-year cycle of recruitment supported a relatively high and stable population because the average recruitment was higher with 4-year cycle of recruitment than without cycle.

Rebuilding time is defined as the total number of years for a population to rebuild to the level associated with MSY after it falls to a very low level (Quinn et al. 1990). Because average rebuilding time from simulations was skewed to the right, median rebuilding time was used. Median time to rebuild a population from a low

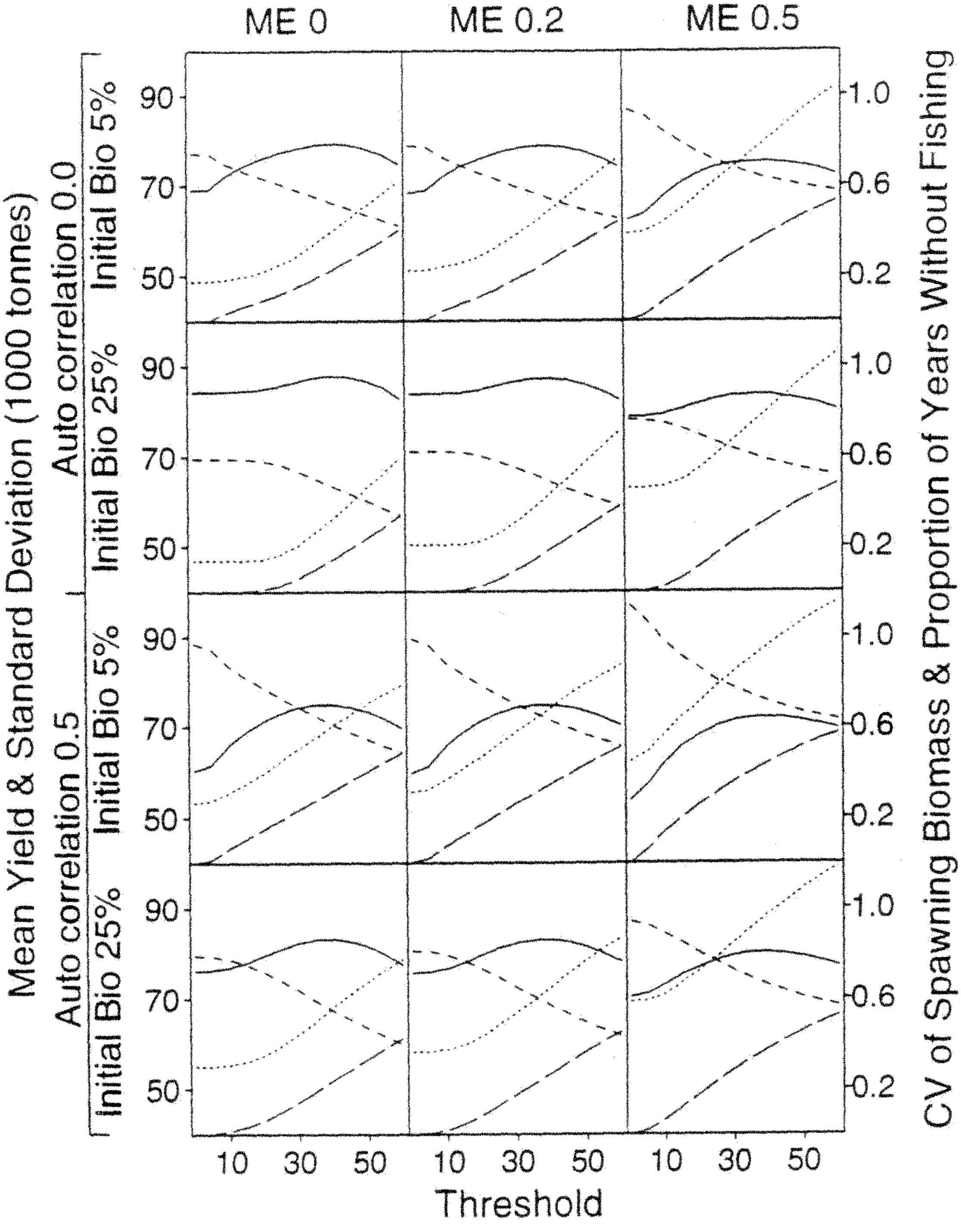

Figure 4.3. Average yield (solid lines), standard deviation (dotted lines), percentage of no fishing (long dashed lines), and CV of spawning biomass (short dashed lines) as a function of threshold level for eastern Bering Sea herring exploited at H_{MSY}. The plots are classified by three levels of measurement error (ME 0, 0.2, 0.5), two levels of autocorrelation (0, 0.5) and two levels of initial biomass (5%, 25%).

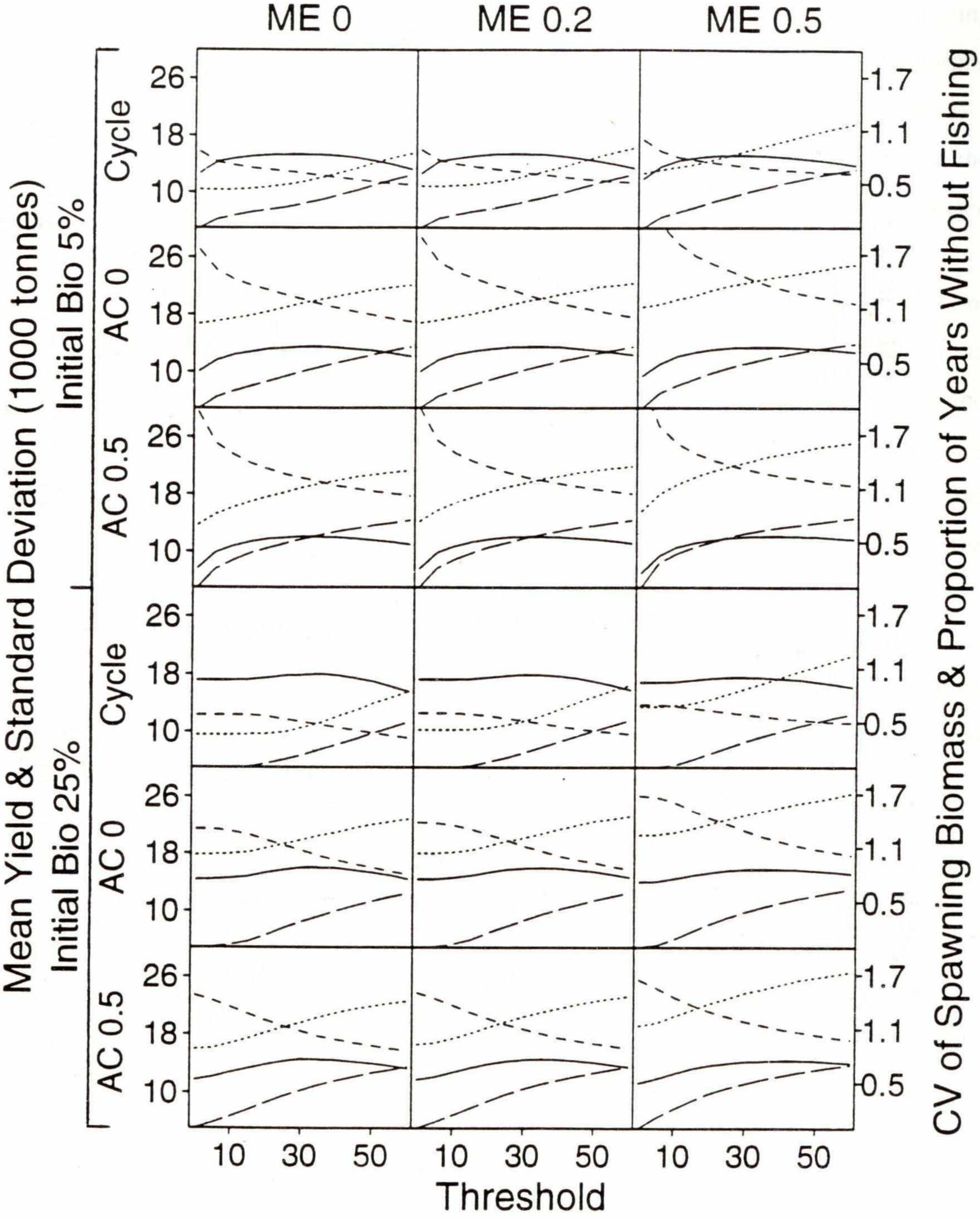

Figure 4.4. Average yield (solid lines), standard deviation (dotted lines), percentage of no fishing (long dashed lines), and CV of spawning biomass (short dashed lines) as a function of threshold level for Prince William Sound herring exploited at H_{MSY}. The plots are classified by three levels of measurement error (ME 0, 0.2, 0.5), three recruitment scenarios (Cycle, AC 0, AC 0.5) and two levels of initial biomass (5%, 25%).

abundance to a threshold level without fishing, called first upcrossing time, was used as a reference to rebuilding time. Without fishing, it took about 8-9 years for EBS herring and 14-15 years for PWS herring to rebuild from 5% of pristine biomass to the biomass associated with MSY (Figure 4.5). With a 20% exploitation rate and no thresholds, the rebuilding time ranged from 12 to 15 years for EBS herring and from 16 to 24 years for PWS herring. With an exploitation rate of H_{MSY} or higher and no thresholds, it took a much longer time to rebuild an overexploited population. Threshold approaches greatly shortened the rebuilding time, especially when the population was heavily exploited (Figure 4.5). The shorter rebuilding time for EBS herring partially results from the steeper slope of its stock-recruitment curve. As expected, the population was rebuilt faster under scenarios with the strong 4-year cycle of recruitment than with no-cycle for PWS herring. Overall, measurement error and environmental autocorrelation increased the rebuilding time.

The optimal levels of threshold and exploitation rate were determined by examining the response surface formed by values of the objective function over a grid of thresholds and exploitation rate ranges. EBS herring was examined with two levels of environmental autocorrelation, three levels of weighting factors, an initial biomass of 5%, 3 levels of measurement error, and no implementation error (Figure 4.6). To illustrate results on a common scale, I show the results as contour plots of the objective function for each scenario scaled to a maximum value of 1 as a function of exploitation rate and threshold level.

The optimal threshold level and exploitation rate declined as a function of the weighting factor λ and measurement error and were fairly robust to variations in the other factors (Figure 4.6). That is, when the variation in yield is weighed more heavily or the population biomass cannot accurately be estimated, a low threshold and a low exploitation rate would be chosen. Environmental autocorrelation influenced the optimal threshold and exploitation rate differently with different weighting factors. When λ = 0, the maximum yield criterion, environmental autocorrelation increased the optimal exploitation rate and average yield by using thresholds. When λ = 0.5 (equal trade-off

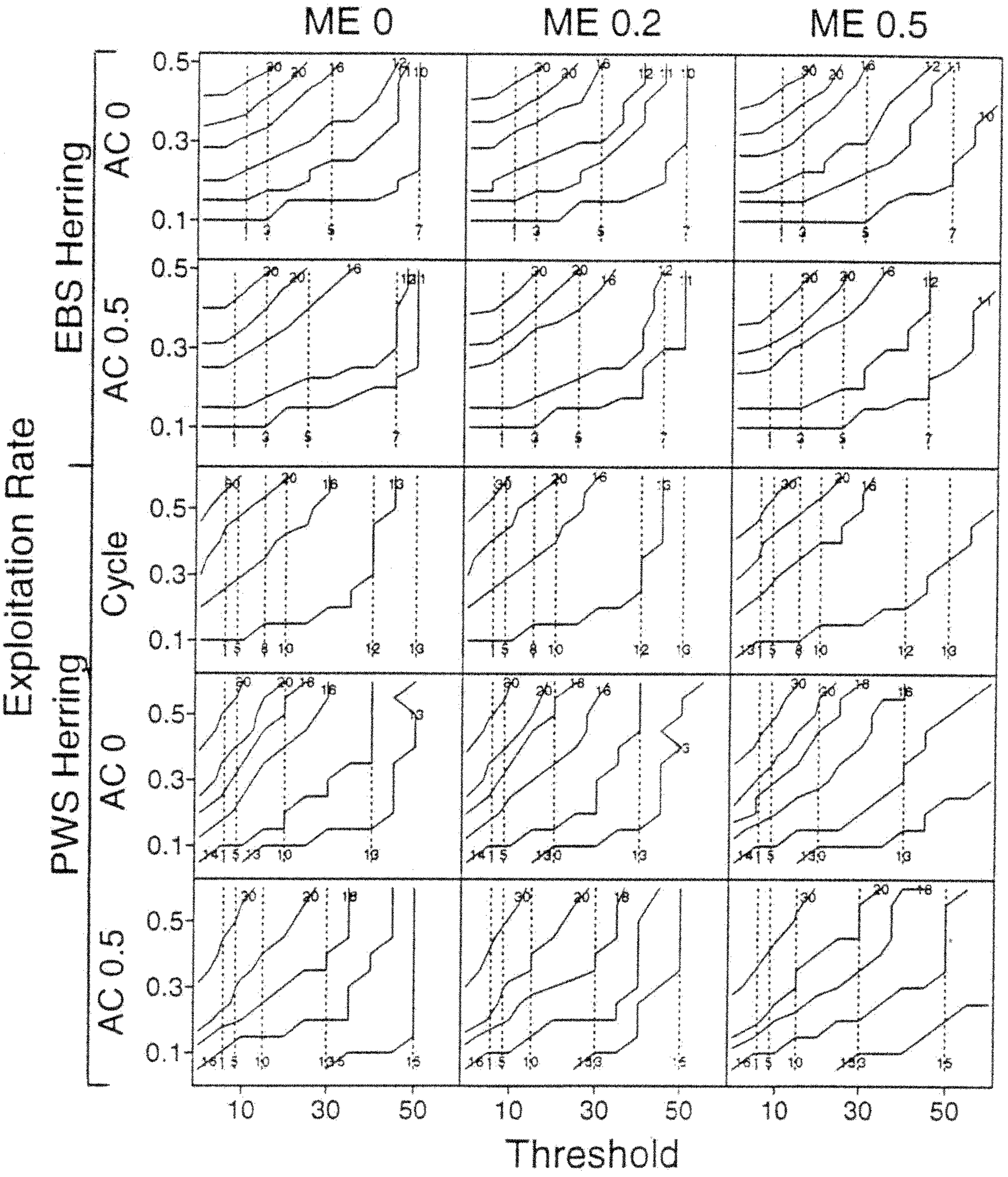

Figure 4.5. Contour plots of median rebuilding time (solid lines) and median time to rebuild to a threshold level (dotted lines) in year as a function of threshold level and exploitation rate for eastern Bering Sea (EBS) and Prince William Sound (PWS) herring. The plots are also classified by three levels of measurement error (ME 0, 0.2, 0.5) and three recruitment scenarios (Cycle, AC 0, AC 0.5).

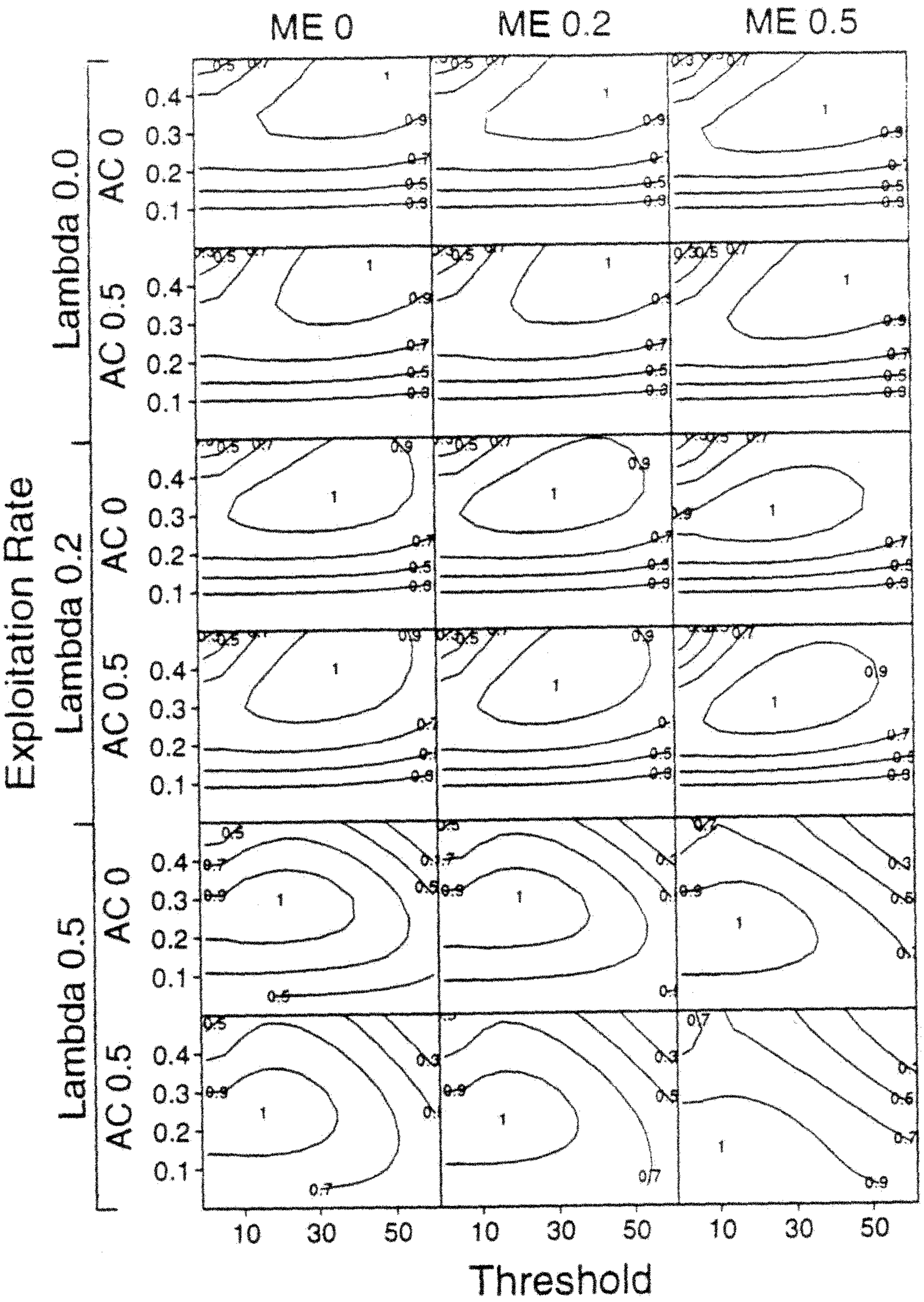

Figure 4.6. Contour plots of the objective function values as a function of exploitation rate and threshold level for eastern Bering Sea herring. The plots are classified by three penalty weighting factors (λ), three levels of measurement error (ME), and two levels of autocorrelation (AC). Initial biomass was 5%. The contour values were scaled from the minimum value (0) to the maximum value (1).

between average yield and variation in yield), environmental autocorrelation decreased both the optimal threshold level and exploitation rate. Combinations of a large implementation error and a large weighting factor (λ=0.5) slightly reduced the optimal thresholds and exploitation rates. In other cases, optimal levels of thresholds and exploitation rate were independent of implementation error.

For EBS herring under the maximum yield criterion, $\lambda = 0$, the optimal threshold levels generally varied from 40% to 50% of pristine biomass and the optimal exploitation rates varied from 35% to 45% among scenarios (Figure 4.6, Table 4.3). For each scenario, there was a broad region between the 0.9 contour and the maximum point at 1, which represents the combinations of the two parameters that would produce approximately 90% or greater of the maximum yield possible (Figure 4.6). This suggests that several combinations could produce close to the maximum yield. For lower values of exploitation rate, the contour lines are flat, indicating that the threshold level has little effect when exploitation rate is small. For the status quo 20% exploitation rate, optimal thresholds were about 25%, 75% or more of the average maximum catch was obtained and less variation occurred (Table 4.3). If the exploitation rate was increased to 31%, i.e., $H_{0.1}$, above 93% of the average maximum catch was obtained with an optimal threshold of about 35%, but with much higher variability. Under the H_{MSY} exploitation rate, above 97% of the average maximum catch could be achieved with an optimal threshold level of 40%.

For the equal trade-off criterion, corresponding to $\lambda = 0.5$, the optimal threshold levels generally varied from 10% to 20% of pristine biomass, and the optimal exploitation rates ranged from 15 to 30% among scenarios for EBS herring (Table 4.3). The contour lines closed off the upper right-hand corner, which eliminates the combinations of both high thresholds and exploitation rates from being the optimal choice (Figure 4.6).

Optimal combinations of threshold levels and exploitation rates were evaluated for PWS herring with an initial biomass of 5% and no implementation error (Figure 4.7). The overall effects of measurement error and the weighting factor on the optimal

Table 4.3. Optimal combinations of threshold levels (T) and exploitation rates (OH) and associated levels of average yield (Y) and standard deviation (SD), and optimal threshold levels and the percentages of their objective values (Obj%) compared to the optimal objective values under a given exploitation rate. Results are shown for an initial biomass of 5% and no implementation error.

Factor				Optimal Combination				H = 0.2		$H = H_{0.1}$		$H = H_{MSY}$	
SN	λ	ME	AC	OH	T	Y	SD	T	Obj%	T	Obj%	T	Obj%
EBS	0.0	0.0	0.0	0.45	50	80.97	78.46	25	75.6	35	94.7	40	98.2
EBS	0.0	0.0	0.5	0.45	45	77.55	82.78	25	75.0	35	93.3	40	97.2
EBS	0.0	0.2	0.0	0.40	45	79.83	73.38	25	77.4	35	96.0	40	99.0
EBS	0.0	0.2	0.5	0.45	45	76.93	87.20	25	76.3	35	94.0	40	97.7
EBS	0.0	0.5	0.0	0.35	40	75.42	79.94	20	85.1	30	99.0	40	99.8
EBS	0.0	0.5	0.5	0.40	45	72.19	95.01	25	84.2	35	98.2	40	99.7
EBS	0.2	0.0	0.0	0.35	35	78.99	56.81	20	83.5	30	98.6	35	99.8
EBS	0.2	0.0	0.5	0.40	35	76.29	71.96	20	85.0	30	98.0	35	99.7
EBS	0.2	0.2	0.0	0.35	30	78.17	58.65	20	84.9	30	99.0	30	99.7
EBS	0.2	0.2	0.5	0.35	30	74.23	68.97	20	86.2	30	98.7	30	99.9
EBS	0.2	0.5	0.0	0.30	25	74.37	66.96	20	91.0	25	99.7	30	97.8
EBS	0.2	0.5	0.5	0.30	25	70.09	75.54	20	92.1	25	99.8	35	98.8
EBS	0.5	0.0	0.0	0.30	20	74.77	47.82	15	96.0	20	99.5	20	96.6
EBS	0.5	0.0	0.5	0.25	15	64.95	50.69	15	98.9	20	98.4	20	95.4
EBS	0.5	0.2	0.0	0.30	20	75.00	51.16	15	97.3	20	99.4	20	96.2
EBS	0.5	0.2	0.5	0.23	15	62.98	51.25	15	99.6	15	97.6	15	94.0
EBS	0.5	0.5	0.0	0.22	15	67.10	55.40	15	99.8	15	96.2	15	91.2
EBS	0.5	0.5	0.5	0.15	10	50.43	48.48	10	98.5	10	91.6	10	87.4
PWS	0.0	0.0	Cyc	0.55	35	16.42	15.03	20	62.6	30	93.4	30	94.7
PWS	0.0	0.0	0.0	0.60	40	16.17	33.76	20	60.8	35	88.1	30	82.1
PWS	0.0	0.0	0.5	0.60	40	14.83	28.55	25	58.5	35	86.2	30	79.8
PWS	0.0	0.2	Cyc	0.60	40	16.37	18.12	20	63.5	30	93.8	30	95.2
PWS	0.0	0.2	0.0	0.60	45	15.85	33.51	20	62.7	35	89.6	30	83.8
PWS	0.0	0.2	0.5	0.60	45	14.67	29.92	25	59.9	35	87.2	30	81.0
PWS	0.0	0.5	Cyc	0.45	30	15.35	16.95	15	71.3	30	98.7	30	99.2
PWS	0.0	0.5	0.0	0.55	60	14.32	35.49	20	72.5	35	96.9	35	92.7
PWS	0.0	0.5	0.5	0.60	50	13.53	32.83	25	67.7	45	93.6	40	88.2

Table 4.3 (continue)

Factor				Optimal Combination				H = 0.2		H = $H_{0.1}$		H = H_{MSY}	
SN	λ	ME	AC	OH	T	Y	SD	T	Obj%	T	Obj%	T	Obj%
PWS	0.2	0.0	Cyc	0.50	25	16.05	12.46	15	73.1	25	97.5	25	98.3
PWS	0.2	0.0	0.0	0.35	25	13.36	18.96	15	88.9	30	99.6	25	99.7
PWS	0.2	0.0	0.5	0.55	30	14.13	25.16	15	85.6	25	98.1	25	95.9
PWS	0.2	0.2	Cyc	0.50	25	16.04	13.31	15	74.6	20	98.1	25	98.7
PWS	0.2	0.2	0.0	0.35	25	13.38	19.28	15	89.4	30	99.9	25	99.8
PWS	0.2	0.2	0.5	0.50	30	13.66	24.51	15	87.1	25	99.0	25	97.1
PWS	0.2	0.5	Cyc	0.40	20	15.06	14.52	15	81.4	20	100	20	99.6
PWS	0.2	0.5	0.0	0.30	20	12.57	18.65	15	93.2	30	97.1	25	99.4
PWS	0.2	0.5	0.5	0.35	25	11.87	21.86	15	92.6	30	99.8	25	99.9
PWS	0.5	0.0	Cyc	0.35	15	14.36	9.83	10	93.9	15	99.8	15	99.3
PWS	0.5	0.0	0.0	0.05	5	3.14	2.94	10	90.5	15	63.2	15	72.2
PWS	0.5	0.0	0.5	0.05	5	2.86	3.28	5	79.7	5	62.9	5	67.3
PWS	0.5	0.2	Cyc	0.35	15	14.44	10.40	10	95.2	15	99.5	15	99.0
PWS	0.5	0.2	0.0	0.05	5	3.19	3.09	10	89.4	15	63.5	10	71.5
PWS	0.5	0.2	0.5	0.05	5	2.90	3.43	5	77.7	5	61.0	5	65.1
PWS	0.5	0.5	Cyc	0.25	10	12.49	10.72	10	99.8	10	94.8	10	93.6
PWS	0.5	0.5	0.0	0.05	5	3.43	3.84	10	81.7	10	55.0	10	63.4
PWS	0.5	0.5	0.5	0.05	0	3.09	4.19	5	69.1	0	44.2	5	56.3

Abbreviation:

Cyc: Four-year cycle of strong recruitment for PWS herring.

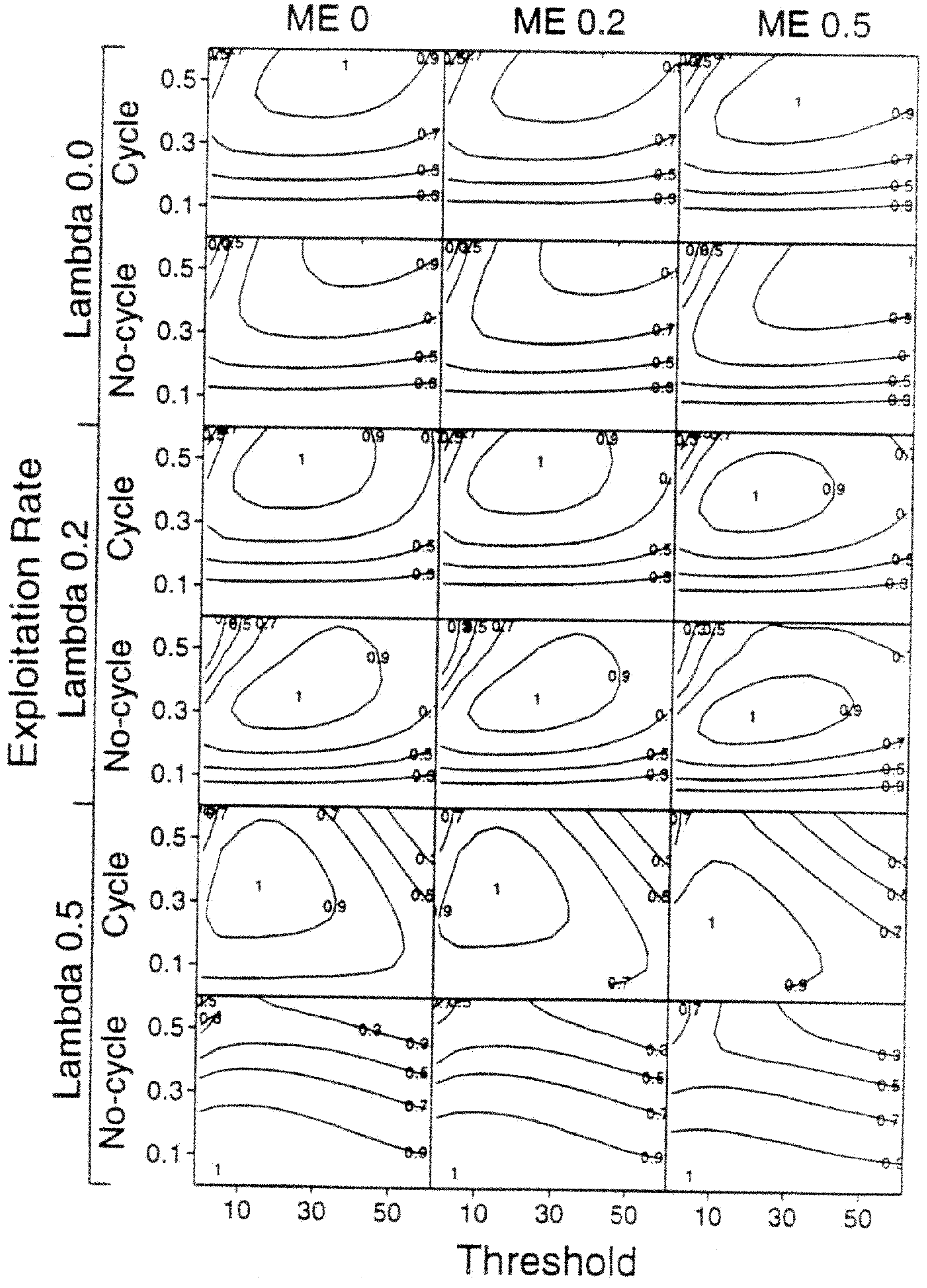

Figure 4.7. Contour plots of the objective function values as a function of exploitation rate and threshold level for Prince William Sound herring. The plots are classified by three penalty weighting factors (λ), three levels of measurement error (ME), and two sets of stock-recruit curves (Cycle, No-cycle). Initial biomass was 5% and no autocorrelation was assumed. The contour values were scaled from the minimum value (0) to the maximum value (1).

levels were similar to those for EBS herring. Because of a high standard deviation of catch, the objective function values were close to zero or negative in scenarios with no-cycle in recruitment and a weighting factor of 0.5, which suggested that the optimal results were almost equivalent to total fishery closures (Figure 4.7).

For PWS herring under the maximum yield criterion ($\lambda = 0$), the optimal threshold levels varied from 30% to 60%, and the optimal exploitation rates ranged from 45 to 60% among scenarios (Table 4.3). For the status quo exploitation rate of 20%, optimal thresholds were 15 to 25%, and more than 58% of the average maximum catch could be obtained (Table 4.3). If $H_{0.1}$ exploitation rate was used, more than 86% of the average maximum catch was obtained with optimal thresholds ranging from 30 to 45%. Under H_{MSY} exploitation rate, more than 80% of the average maximum catch could be achieved with optimal threshold levels from 30 to 40%.

With $\lambda = 0.2$, the highest contour values are associated with intermediate threshold levels and high exploitation rates (Figure 4.7). Optimal threshold levels were quite robust: 15% and 25% with 20% and H_{MSY} exploitation rates, respectively (Table 4.3).

For the equal trade-off criterion, the optimal threshold levels were 10% or 15%, and the optimal exploitation rates ranged from 25 to 35% among scenarios for PWS herring with the 4-year recruitment cycle (Figure 4.7). When no-cycle in recruitment occurred, both the optimal threshold levels and exploitation rates were 5% or less due to large standard deviations of yield.

DISCUSSION

A threshold management strategy aims to conserve fish stocks, minimize the risk of collapse of a fishery, and to enhance long-term productivity of a population. However, over the short-term, such a policy increases the probability of economic hardships for the fishing industry and fishing communities caused by closed fisheries. Therefore, optimal threshold levels have to be determined by a trade-off among benefits and costs. In this study, this trade-off was handled by choosing a weighting factor λ.

Certainly, the choice of λ value is subjective, but most likely λ ranges from 0 to 0.5. In principle, fisheries management policies in Alaska traditionally favor a small weighting factor, i.e., more weight is placed in protecting resources and maximizing sustainable yield.

Optimal threshold levels from this study ranged from 10% to 40% of the pristine biomass for EBS herring and from 0 to 60% for PWS herring. The threshold values depended upon the trade-off between the increase of yield and the decrease of variability in yield and exploitation rates. The response surfaces of the objective function values were fairly flat, i.e., several combinations of exploitation rate and threshold level could produce close to the maximum objective value possible. This property of the objective function could increase management flexibility. Under the status quo exploitation rate of 20% and the maximum yield criterion, optimal thresholds varied from 20 to 25% for EBS herring and from 15 to 25% for PWS herring, but increases in average yield by using a threshold were small. With all factors and population models considered in this study, a threshold of 25% of pristine biomass provides a safeguard for protecting the herring populations and approximately maximizes the sustained yields under a 20% exploitation rate.

The current threshold levels for most of the herring stocks in Alaska are about 20-25% of the average observed biomass. The average observed biomass is likely less than the pristine biomass defined in this study. Thus, thresholds used in current herring management plans may be somewhat lower than optimal levels for maximizing average yield. Estimation of pristine mature biomass is as important as definition of a percentage for threshold level. The most current data should be examined to estimate pristine biomass before setting thresholds. Incidentally, this study validated the threshold of 25% of pristine biomass set arbitrarily for British Columbia herring stocks (Hall et al. 1988).

Under the maximum yield criterion, optimal exploitation rates were almost always higher than H_{MSY}. Combinations of high threshold levels and exploitation rates approximated pulse fishing and resulted in maximum average yield, but with very high variation. Yet the gain in yield was very little with an exploitation rate exceeding H_{MSY}.

As with previous studies on Pacific herring management strategies (Funk 1991; Fried and Wespestad 1985; Hall et al. 1988), exploitation rates $H_{0.1}$ and H_{MSY} were much higher than the status quo exploitation rate of 20%. The status quo exploitation rate resulted in 75%-85% and 59%-73% of the maximum yield possible for EBS and PWS herring, respectively, with much less annual variation. Moreover, under the status quo exploitation rate, the spawning biomass was less variable and the chance of closing a fishery was much lower than under exploitation rates $H_{0.1}$ and H_{MSY}. Unless the management objective is solely to maximize average yield, it is not beneficial to move the exploitation from the status quo to $H_{0.1}$ or H_{MSY}.

Species interactions and depensatory predation mortality were not considered in this study. Wespestad (1991) showed that EBS herring abundance is negatively associated with EBS pollock abundance. Kajimura (1984) indicated that Pacific herring is an important prey for northern fur seals along the coasts of Washington, British Columbia, and Southeast Alaska. Haist et al. (*in press*) demonstrated that the fisheries data of British Columbia herring are statistically better fitted with depensatory natural mortality than with a constant natural mortality, and that maximum sustainable exploitation rate is lower with a depensatory natural mortality than with a constant mortality. Collie and Spencer (*in press*) applied a model with depensatory predation to Sitka Sound herring and concluded that MSY occurred at fishing mortality of 0.2 for the threshold policy. With the uncertainty of species interaction, the status quo exploitation rate plus a threshold of 25% of pristine biomass may be a safe approach for Alaska herring stocks. Further study on the optimal harvest strategies of Alaska herring could yield insight by evaluating the consequences of different sets of assumptions about species interactions.

Alternative objective functions for herring roe fisheries management include maximizing roe production and maximizing economic return. Because the roe production of Alaska herring was approximately a linear function of the body weight (Linda Brannian, Alaska Department of Fish and Game, personal communications), maximizing yield was close to maximizing roe production. Roe from old, large herring is generally more valuable than from young, small herring. Funk (1991) addressed this economic problem and concluded that the exploitation rates corresponding to the objectives of maximizing yield and maximizing economic return are similar for EBS herring and only slightly different for PWS herring. Although the unit price of roe from large herring is higher than that from small herring, the total economic return is not necessary higher because many herring die off before they have an opportunity to grow to a large size. On the other hand, when multiple users share a fisheries resource, maximizing economic return is seldom the sole management objective. Equitable allocation among different user groups outweighs the maximum economic return. Herring fisheries in Alaska are such a case.

Successful threshold management strategies depend highly on accuracy of population estimates. Two kinds of measurement error likely occur: random and systematic errors. Random measurement error was examined in this study and could reduce both optimal thresholds and exploitation rates. Spawn deposition surveys used to estimate absolute herring abundance in PWS may result in standard deviations of random measurement errors between 0.2 and 0.5 (Schweigert et al. 1985), as defined in this study. Systematic bias may occur from aerial surveys. Peak biomass estimated from aerial surveys may represent a fraction of total mature biomass because migrations to and from the spawning grounds are spread over time and because poor weather often reduces visibility during surveys. For EBS herring primarily in the Togiak area, aerial surveys substantially underestimated spawning biomass during the mid-1980's (Baker 1991; Wespestad 1991). Effectively, this reduces the maximum exploitation rate of 20% to a smaller percentage. Systematic measurement error reduces not only average yield, but also the effectiveness of threshold management strategies. A threshold is not needed when the exploitation rate is very small.

Results of this study indicated that implementation error had relatively minor effects on optimal threshold levels for Alaska herring. The most important effect of implementation error on management strategies was to reduce the optimal threshold levels and exploitation rates slightly when heavy weight was given to the variation in yield, because implementation error increased the variation in yield. Implementation error was assumed to have a mean of zero, but actual herring catches in Alaska are often slightly above the catch quota, which results in a positive mean for implementation error (Funk and Zheng 1992b). The skewed implementation error does not alter the conclusions of effects of implementation error on optimal threshold levels, but it affects optimal exploitation rates. The positively skewed error cancels out a small proportion of exploitation rate, and thus, optimal exploitation rates are a little lower than those with an unskewed implementation error.

A stock-recruit relationship is a key element of long-term harvest strategies. Optimal thresholds are sensitive to this relationship (Quinn et al. 1990). Commonly, Ricker curves have been fitted to herring stock-recruit data (e.g., Hall et al. 1988; Stocker et al. 1985; Stocker and Noakes 1988; Winters and Wheeler 1987). Density of herring egg masses is generally related to spawning biomass, the survival and development of eggs are inversely associated with egg density, and maximum larval production occurs at medium egg densities (Taylor 1971). Together, these relationships suggest a dome-shaped stock-recruit model. Furthermore, cannibalism in Pacific herring is not uncommon (Grosse and Purcell 1990).

But environmental noises are so large that spawning biomass could explain only a small proportion of recruitment variation. Environmentally stratified stock-recruit curves were applied to Atlantic herring (*Clupea harengus*) (Anthony and Fogarty 1985) and prawn (Penn and Caputi 1986; Tang et al. 1989). The occurrence of strong herring recruitment every 4 years in the Gulf of Alaska since 1976 is most likely induced by the variation of oceanographic conditions. Alternative explanations are that recruitment cycles may result from oceanographic factors interacting with the dynamics of the stock, or simply from the biology of the stock (Murphy 1968). Whatever the mechanism, these herring populations primarily consist of two age groups, and stocks are very vulnerable to overfishing. Whether this 4-year cycle continues to hold has important consequences to herring fisheries management in the future.

Multiple herring stocks have been managed separately in the EBS according to their spawning locations. Thus, the threshold biomass for EBS herring has to be divided for each substock according to the stock size. If EBS herring stocks all have similar stock-recruit relationships, the conclusions about herring threshold management strategies based on the assumption of a single stock in the EBS will still hold. Furthermore, because of multi-stock management, it is unlikely that all stocks would fall below a threshold level at the same time; thus, the impact of threshold closures on harvest opportunities would be less than that under a single-stock management strategy.

Chapter Five

COMPARISON AND EVALUATION OF THRESHOLD ESTIMATION METHODS FOR EXPLOITED FISH POPULATIONS

SUMMARY

Previous studies (Chapters 3 and 4) have shown that threshold management policies for single-species systems are robust and close to optimal in regard to the class of all common policies. Application of these policies to fisheries management requires developing methods of threshold estimation and evaluating alternative threshold specifications on fish population dynamics and yields. Simulated age-structured populations were used to compare and evaluate seven threshold estimation methods for pollock and herring populations in the eastern Bering Sea (EBS). Parameters for these two populations were obtained from cohort analysis, catch-at-age analysis and catch sampling. The seven threshold estimation methods are: default percentages of pristine biomass, Fowler's rule, May's method, surplus production model, depensatory production model, stock-recruit model, and spawning biomass per recruit. Passively adaptive simulations were conducted in which threshold levels were updated and applied to fisheries management each year. Influences of several factors on threshold estimation methods were examined. Several statistics were collected as criteria for comparison and evaluation. It was found that the default percentages of pristine biomass usually performed best. The estimation procedures of the surplus production model and depensatory production model often failed. The stock-recruitment method could produce large biased threshold estimates with a small data set. May's method usually resulted in high threshold levels that are favored with the objective of maximum yield, and Fowler's rule often produced low threshold levels which are preferred with the equal trade-off criterion. These two methods did not result in reliable estimates of thresholds given parameter uncertainties.

INTRODUCTION

Common harvest strategies include constant catch, constant harvest rate, and fixed escapement strategies (Getz and Haight 1989). The constant catch strategy generates stable yield, but the yield level must be relatively low to sustain the population. With the exception of some fisheries managed by international treaties, this strategy is gradually losing favor. The constant harvest rate strategy gives a good balance between average yield and yield variation (Walters 1986), yet it may not be able to protect a population that drops to a very low level. On the other hand, maximum yield can be obtained under the fixed escapement policy, but the variation in yield is also largest compared to other common strategies (Reed 1979; Getz and Haight 1989).

A compromise between the constant harvest rate and fixed escapement strategies is a threshold management policy, in which harvesting occurs at a constant harvest rate but ceases when a population drops below a critical low level (Quinn et al. 1990). This policy not only produces a good balance between average yield and variation in yield, but also provides a conservative safeguard from overharvesting. Computer simulation studies on EBS pollock (*Theragra chalcogramma*) have shown that a threshold policy always increased average yield over that associated with the constant harvest rate policy, and, in most cases, greatly increased average yield while only slightly increasing variation in yield (Chapter 3; Quinn et al. 1990). An over-exploited population was better protected and more quickly enhanced under the threshold policy than the constant harvest rate policy (Chapter 3; Quinn et al. 1990). Threshold management policies for British Columbia herring fisheries were evaluated and compared with other alternative policies by Hall et al. (1988) and Haist (1990). Their results also indicated that setting a threshold level in a harvest policy would have a positive effect on long term average yield and would help safeguard a population from collapsing by reducing high harvest rates when its abundance is low.

The threshold concept is relatively new in fisheries management and has been primarily applied to species highly vulnerable to environmental variation such as herring (Trumble and Humphreys 1985) and king and Tanner crabs (NPFMC 1990). No studies to date appear to have evaluated threshold estimation methods for exploited populations. Most threshold levels used in fisheries management are set arbitrarily. A threshold of 20% of pristine biomass was analytically derived by Thompson (*in press*) to prevent overfishing for exploited fish populations, but his results were mainly based on a strongly depensatory Beverton-Holt stock-recruitment relationship. Successful application of threshold management policy to fisheries requires developing methods of threshold estimation and evaluating threshold levels under a given management objective.

In this chapter (based on Zheng et al. *in press* b) I compared and evaluated seven methods to estimate threshold levels by using computer simulations. The parameters of simulated age-structured populations are from EBS pollock and herring, two of the most commercially and ecologically important species in the northeast Pacific Ocean. In the simulations I adopted a passively adaptive approach similar to Hilborn (1979), in which available data were used to update threshold levels, and the updated thresholds were applied to harvest management each year. Effects of measurement errors and implementation errors on threshold estimation were investigated. Evaluation criteria included average yield, standard deviation of yield, mean threshold levels, variation of estimated thresholds and spawning biomass, and percentage of years without fishing.

METHODS

Age-structured Model

Typical age-structured single-species models were used in this study. The models and population parameters for EBS pollock and herring were described by Quinn et al. (1990) and Zheng et al. (*in press* a). Recruitment for both stocks was modelled by Ricker curves and lognormally distributed environmental noises. The main differences between the pollock and herring models were that fishing mortality and total number of eggs as a spawning index were applied to pollock, and exploitation rate and spawning biomass as a spawning index to herring.

Threshold Estimation Methods

Seven alternative methods were investigated to estimate threshold levels. Each method has two parameters to be estimated during simulations.

1. Default percentage of pristine biomass. Thirteen levels ranging from 0 to 60% were examined. This method requires estimates of a pristine biomass, which is defined as the average biomass over a long period under average environmental conditions without fishing. Each simulated year, the parameters of a Ricker stock-recruit model were estimated using the available data, and an age-structured model was simulated for 150 years in the absence of fishing mortality, and the biomasses during the last 100 years were averaged to estimate the pristine biomass under this new set of population parameters.

2. Fowler's rule. If the approximate shape of a fish population growth curve is known, a threshold can be established in the absence of detailed stock-recruitment data because differently-shaped growth curves are known to produce well-defined quantitative differences in the dynamics of the population. The shapes of population growth curves can be determined by the locations of their inflection and peak points. The inflection point is an important biological reference point at which the maximum growth rate occurs. The location of the inflection point can be used as a threshold level. This method is applicable to a population with high fecundity whose stock-recruit curve peaks sharply near the origin. Fowler (1981, 1988) showed that the shapes (inflection points) of known growth curves for fish, mammals, insects and protozoans can be predicted from typical production/biomass ratios for each species via an empirical linear regression:

(5.1) $\mathrm{TP} = a + b \ \mathrm{Ln}(\mathrm{MSY}/B_{\mathrm{MSY}})$,

where TP is threshold level (percentage of pristine biomass), B_{MSY} is biomass at maximum average sustainable yield (MSY), and a and b are parameters estimated from empirical data, equal to 0.11 and -0.074 for fish, respectively. Because I did not use stock-recruit data for this method, I estimated production/biomass ratio at the MSY level and pristine biomass through a surplus production model similar to Quinn et al. (1984)

during simulations.

3. May's method. Thresholds can be estimated from life-history and environmental parameters of a fish stock through a resource-consumer approach. This strategy was developed by MacArthur (1972) and applied to fish by Rothschild (1986). May (1980) proposed using this approach to determine a critical stock density (B_{MSY}) below which stock collapse is likely, and he provided an explicit equation for this threshold in a model system based on a Beverton-Holt stock-recruit relationship.

Let M be instantaneous natural mortality, r the intrinsic population growth rate of a conventional logistic equation, and υ the coupling coefficient representing the effective strength of the coupling between the resource and its consumer, then

(5.2) $\mathrm{TP} = [(1 + \tau)^{0.5} - 1]/\tau$,

where $\tau = (1 - \upsilon)/(\upsilon + M/r)$.

It is difficult to estimate the coupling coefficient υ, which relates the consumption rate of a consumer to the renewable rate of its resource. υ was arbitrarily set to 0.45 and 0.28 for EBS pollock and herring, respectively. M is approximated as 0.3 for pollock and 0.25 for herring. Parameter r and pristine biomass were estimated during simulations by a surplus production model.

4. Stock-recruit model. If a stock-recruit model is known, a threshold level can be defined in terms of the slope of the curve. Egg number or spawning biomass corresponding to an equilibrium point on the stock-recruit curve with slope of 10% of the slope at the origin is used as a threshold (Sissenwine and Shepherd 1987). The parameters of the Ricker stock-recruit function were estimated each year during simulations.

5. Spawning biomass (eggs) per recruit. Spawning biomass per recruit can be used as a basis for thresholds and has been implemented in fisheries management by ICES (1984) and NEFMC (1985). Sissenwine and Shepherd (1987) gave another option for this method. This method is more suitable for selecting a fishing mortality when a stock-recruit function is not available (Clark 1991; Thompson *in press*). To be

compatible with other threshold methods in the simulation framework, a biomass threshold was adopted. Before starting simulations, a spawning biomass per recruit of 20% of the pristine value was used to compute a threshold fishing mortality. During simulations, a stock-recruit function was fitted each year to estimate the equilibrium spawning biomass corresponding to the threshold fishing mortality. This equilibrium spawning biomass was used as the biomass threshold.

6. Surplus production model. The traditional surplus production model can be modified to incorporate a threshold parameter that corresponds to a biomass level below which the productivity of the population is assumed to be zero (Quinn and Collie 1990). The relation between equilibrium yield Y_* and biomass B_* is

(5.3) $Y_* = [4m/(B_\infty - T)](B_* - T) - [4m/(B_\infty - T)^2](B_* - T)^2$,

where m is MSY, T threshold biomass and B_∞ pristine biomass. Equation (5.3) is easily transformed to a second order polynomial regression by replacing equilibrium yield with annual surplus production (*EASP*) and equilibrium biomass with annual exploitable biomass (*EB*), i.e.,

(5.4) $EASP_t = b_0 + b_1 EB_t + b_2 EB_t^2$.

Solving equations (5.3) and (5.4) results in estimates of T and B_∞:

(5.5) $T = [-b_1 + (b_1^2 - 4b_0b_2)^{1/2}]/ 2b_2$,

and

(5.6) $B_\infty = [-b_1 - (b_1^2 - 4b_0b_2)^{1/2}]/ 2b_2$.

7. Depensatory production model. The traditional surplus production model can be further modified to include a depensatory effect. The estimated biomass level, below which the productivity of a population would be negative, can be used as a threshold (Clark 1976):

(5.7) $Y_* = rB_*(B_*/T - 1)(1 - B_*/B_\infty)$.

Replacing equilibrium yield with *EASP* and equilibrium biomass with *EB* results in a polynomial regression of order 3 with an intercept equal to 0, or,

(5.8) $EASP_t = b_1 EB_t + b_2 EB_t^2 + b_3 EB_t^3$.

Threshold and pristine biomass are estimated as

(5.9) $T = [-b_2 + (b_2^2 - 4b_1b_3)]/2b_3$,

and

(5.10) $B_\infty = b_1/(b_3T)$.

Simulations

Hilborn (1979) gave a comprehensive description of the use of computer simulations to test alternative management policies. I followed his approach to simulate a fishery management process using feedback estimation and control. Figure 5.1 illustrates the flow diagram of computer simulations used to compare and evaluate alternative threshold estimation methods. Two sets of simulations were constructed. For the first set, I selected an initial condition and a fishing period of 15 years with fishing mortalities randomly chosen from a range of 1/2 F_{MSY} to > F_{MSY} such that the average population biomass in year 16 was about 20% of its pristine biomass during each simulation. Equal starting biomass was necessary to compare the diagnostic statistics under different threshold rules. Starting from year 16, F_{MSY} was used, a threshold was estimated, and the fisheries were managed according to the estimated threshold. Each year the same F_{MSY} was used, a new data point was added to the growing database, and the threshold was re-estimated. The process continued until year 65, i.e., the planning horizon is 50 years. From each simulation I compiled statistics on average yield, standard deviation of yield, total time below the threshold level (no fishing), mean and median threshold levels, standard deviation of thresholds, and variation in spawning biomass.

The second set of simulations was constructed to compare variation of estimated thresholds over time. The simulations were the same as the first set except that the initial fishing period was 5 years and thresholds were estimated starting from the sixth year. The same planning horizon of 50 years was used. The main purpose of estimating thresholds starting from the sixth year rather than the sixteenth year was to examine how many years of data were required to stabilize the estimated thresholds.

The parameters of the models, including the seeds for the random generator,

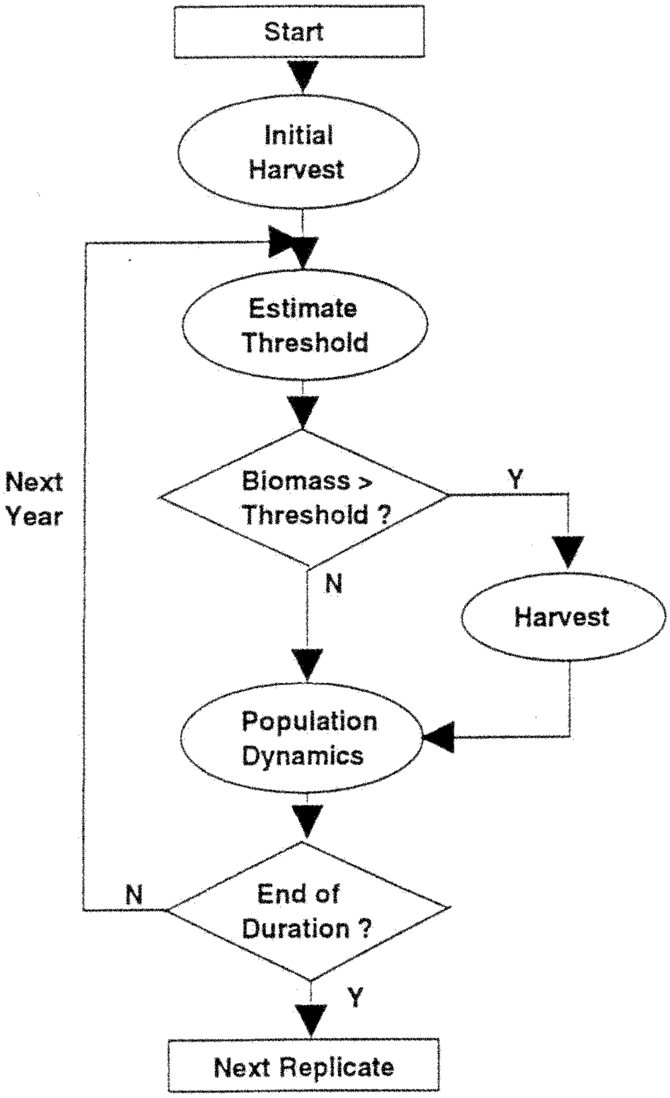

Figure 5.1. Flow chart of computer simulations to compare and evaluate different threshold estimation methods.

were identical for all simulations. After some test runs, 101 replicates were used to ensure consistency of the results for each simulation for the first set of simulations and 200 replicates for the second set of simulations.

Two initial population conditions, pristine and overexploited, were tested. The major difference of the results was that the thresholds estimated by production model methods (Fowler's rule, May's method, surplus production model, and depensatory production model) during the first several years were slightly more variable when starting with the overexploited condition than with the pristine condition. However, when the initial fishing mortality was adjusted so that the biomass was about 20% of the pristine value in year 16, the diagnostic statistics resulting from the overexploited condition were very similar to those obtained from the pristine condition. Therefore, the only results of using pristine biomass as initial biomass are reported.

Measurement errors have a profound effect on the estimated stock-recruit functions and performance of fisheries management policies (Walters and Ludwig 1981). A lognormal distribution is usually assumed for measurement errors (Haist 1990). I examined alternative management policies under three levels of measurement errors with standard deviations 0, 0.2 and 0.5 of the corresponding lognormal distribution and mean 0. The true biomass was multiplied by the measurement error each year to obtain the estimated biomass.

In practice, catch quotas are seldom reached exactly, a phenomenon resulting in implementation error. Implementation errors, which are defined as the differences between the pre-determined catch quota and the actual catch, were incorporated into the simulations for realism and were assumed to follow normal distribution. Three levels of implementation errors with standard deviations of 0, 0.2 and 0.5, and mean 0 were used in the simulations. To prevent extremely large errors from the two tails of the error distributions, measurement errors were truncated by their 95% confidence limits and implementation errors by their 90% confidence limits. If an error was outside its range, it was discarded and a new error was generated.

Some methods failed to estimate threshold levels because they failed to converge for some years during simulations. If a failure occurred, the average of past estimated threshold levels from the same method was used. If this average was not available at the beginning of a simulation, a default threshold of 25% of pristine biomass was adopted.

The same set of simulations was repeated using fixed threshold levels rather than estimating them during simulations. These fixed thresholds were estimated before simulations using the existing population data. By comparing the results under the fixed thresholds with those under re-estimated thresholds during simulations, I was able to quantify the loss of objective function values stemming from estimation errors of thresholds.

Optimal Threshold Criteria

From the simulations it was found that the standard deviation of yield was linearly related to the variation of spawning biomass and percentage of years without fishing. Following Quinn et al. (1990), for the sake of simplicity, I chose a flexible objective function that is a linear combination of average yield and standard deviation of yield. To select the optimal threshold levels, the objective function was maximized over the planning horizon, or

(5.11) $\max[(1 - \lambda)\ Y_{th} - \lambda\ SD_{th}]$.

where Y_{th} and SD_{th} is the average annual yield and standard deviation under threshold management policy "*th*", and λ is a penalty weighting factor.

RESULTS

Frequency Distribution of Estimated Thresholds

A desirable method would estimate threshold levels that are least variable and most robust to measurement and implementation errors. Plots of frequency distributions of estimated thresholds allow the comparisons of the variation and robustness of each method. The estimated thresholds were quite dispersed, especially with methods 'S-R', 'S/R', and 'May' (see Table 5.1 for notation) for EBS pollock (Figure 5.2).

Table 5.1. Summary of notations used in figures.

DepS (D):	depensatory production model
Fowl (F):	Fowler's rule
Lam:	lambda (λ), penalty weighting factor
May (A):	May's method
ME:	measurement error
S-R (E):	stock-recruit model
S/R (R):	spawning biomass per recruit
SB:	spawning biomass
Surp (S):	surplus production model
10%-50% (0-60):	default percentage of pristine biomass as threshold level

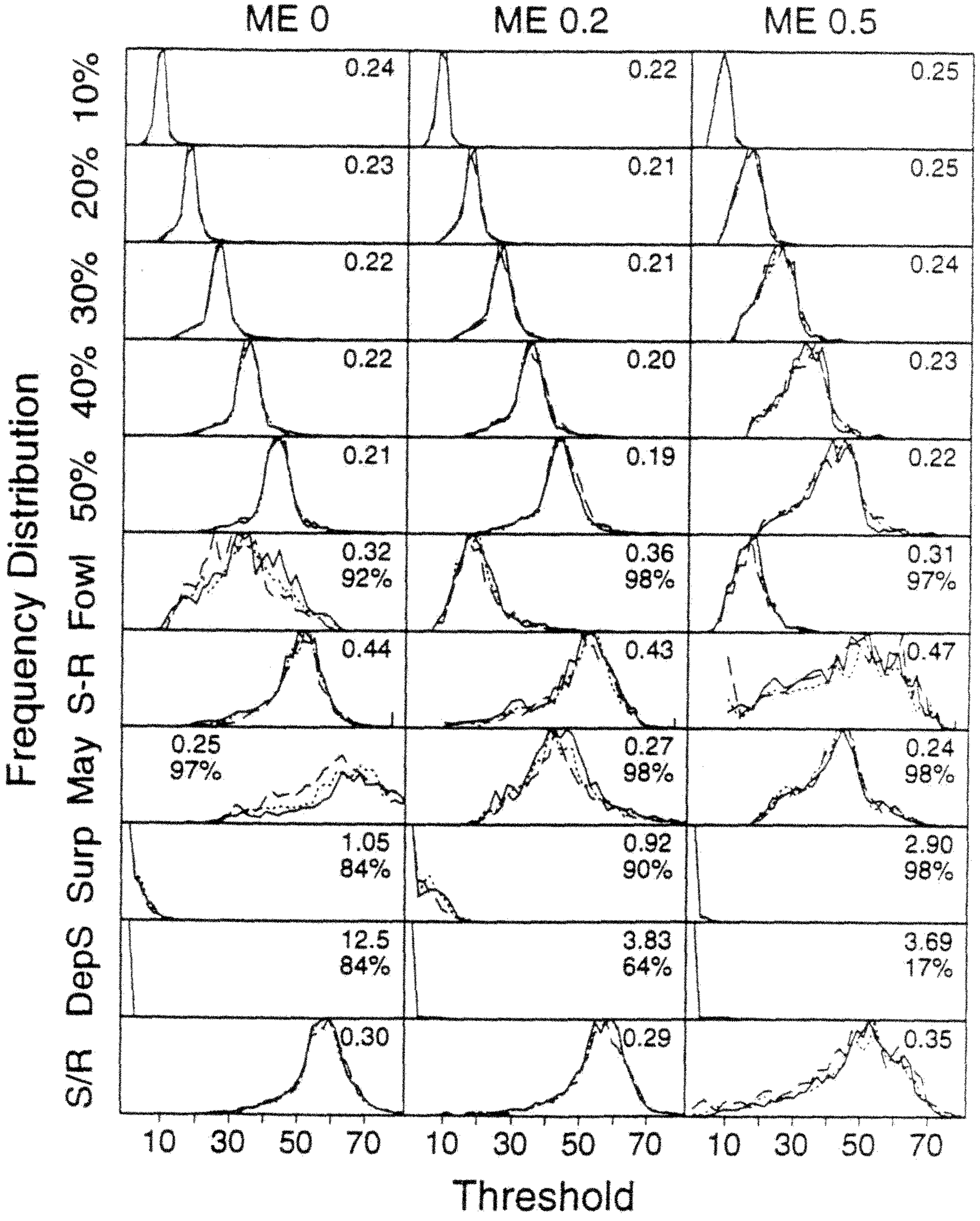

Figure 5.2. Frequency distributions of estimated thresholds by eleven methods (levels) for eastern Bering Sea pollock. Solid lines are for implementation error 0, dotted lines for 0.2, and dashed lines for 0.5. The numerical values are CV of estimation and the percentages are the probability of successful estimation. When this percentage is not shown, it is 100%. See Table 5.1 for notations of threshold estimation methods.

The default percentage method had the least variation of estimated thresholds with CV values ranging from 19% to 25% (Figure 5.2). Higher measurement error (ME 0.5) and lower threshold levels increased the variation. The distributions of thresholds with Fowler's rule and May's method exhibited a common feature: measurement error helped to reduce the variation of estimated thresholds, and higher threshold levels were associated with smaller measurement errors. Both methods depended on the parameters estimated by a conventional surplus production analysis. Thresholds were successfully estimated more than 90% of the time. The stock-recruit and spawning biomass per recruit methods produced the most variable estimates of thresholds, especially under higher measurement errors. The majority of the estimated thresholds were 0 with the surplus production and depensatory production models. This is not surprising, because the models I used for the simulations did not contain zero or negative productivity when spawning biomass was greater than zero. Implementation errors made very little difference in the frequency distributions of thresholds estimated by all seven methods.

The frequency distributions of estimated thresholds for EBS herring were similar to those for pollock with two exceptions (Figure 5.3). First, the thresholds were much more variable and the chances of successfully estimating a threshold for herring were smaller for most methods. This might be caused by the influence of higher environmental noise on recruitment; the environmental noise for herring is double that for pollock. Only Fowler's rule and May's method had similar levels of variation of thresholds to those for pollock. Second, measurement errors increased the variation of estimated thresholds for all methods except the stock-recruit model, spawning biomass per recruit and depensatory production model methods.

Average Yield, Standard Deviation, Percentage of No Fishing, and CV of Spawning Biomass

A good estimation method would not only be robust to noise, but would also maximize yield, minimize variation in yield, stabilize spawning biomass, and minimize the chance of closing a fishery. Figure 5.4 compares these statistics for different

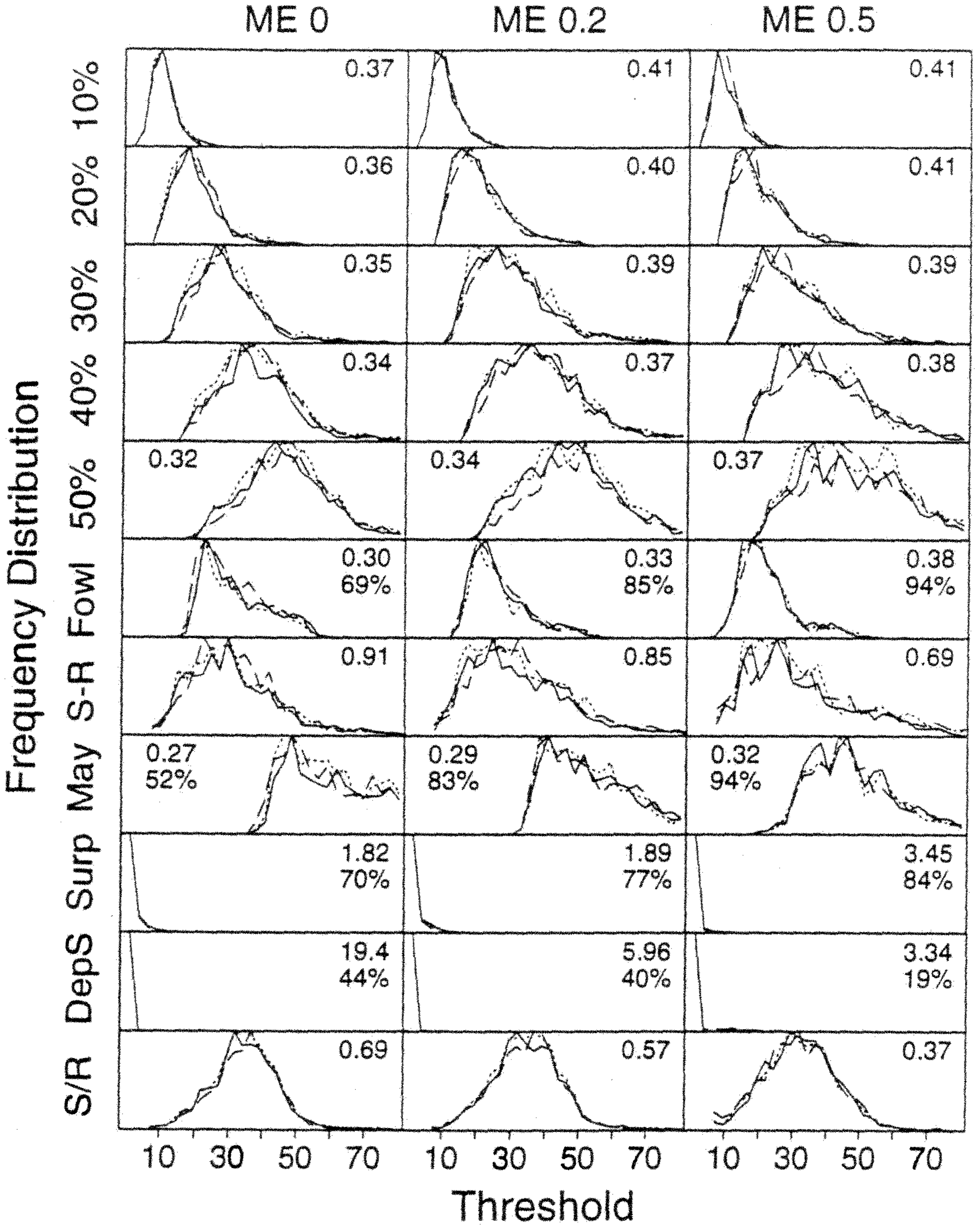

Figure 5.3. Frequency distributions of estimated thresholds by eleven methods (levels) for eastern Bering Sea herring. See the caption 'of Figure 5.2 and Table 5.1 for explanation of the notations.

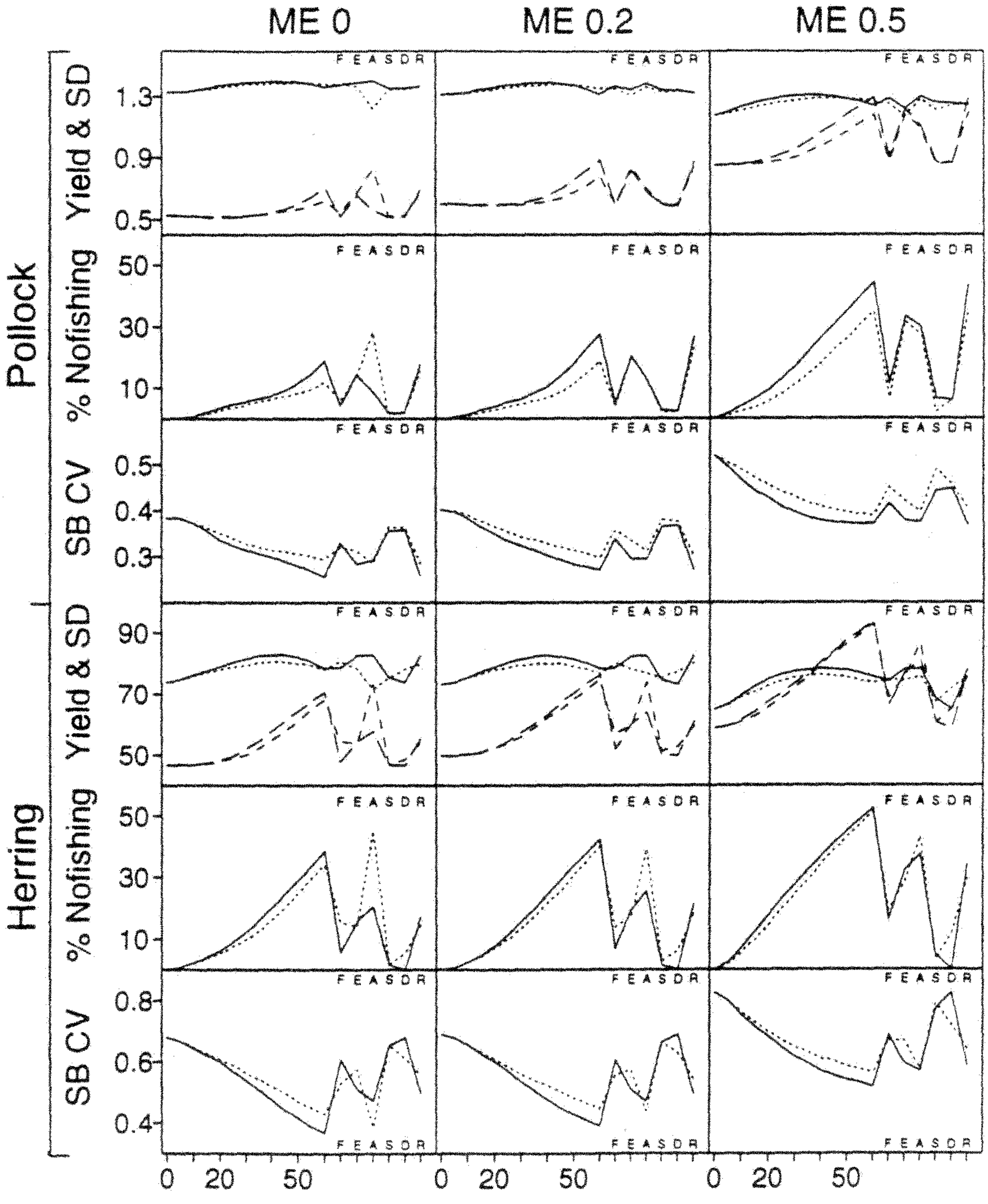

Figure 5.4. Average yield, standard deviation, percentage of years with no fishing, and CV of spawning biomass as a function of 19 threshold methods (levels). Implementation error is zero. Solid and long dashed lines are for simulations with fixed thresholds, and dotted and short dashed lines for estimated thresholds. See Table 5.1 for notations of threshold estimation methods.

estimation methods. Under the method of the default percentage of pristine biomass, maximum average yields occurred at intermediate threshold levels for pollock. These threshold levels were reduced by measurement error. The standard deviations of yield were similar with low threshold levels, then increased quickly when the thresholds were beyond certain levels. For each scenario there existed a threshold level below which the increase of the average yield was greater than the increase in standard deviation of yield. Average yields were slightly less and standard deviations of yield were slightly higher under the scenarios with thresholds being re-estimated during simulations than those scenarios with fixed thresholds. For other alternative methods, average yields and standard deviations of yield were within the range experienced by the default percentage method: May's method had higher yield and higher standard deviation of yield, and Fowler's rule had relatively high yield and low standard deviation of yield. Measurement error decreased the average yields slightly and increased the standard deviations of yield greatly.

The chances of closing fisheries ranged from 0 to 45%, and the coefficients of variation of spawning biomass ranged from 25% to 52% for pollock among all of the estimation methods (Figure 5.4). Measurement error increased these two quantities greatly. The level of the uncertainty of biomass estimation was a very important factor influencing how often a fishery would be closed. For a given level of measurement error, a high threshold level generated a high percentage of years of no fishing and a low coefficient of variation of spawning biomass. Closing a fishery would increase the variation of yield but stabilize the spawning population. Therefore, the percentage of years of no fishing was positively associated with the standard deviation of yield and negatively associated with the coefficient of variation of spawning biomass (Figure 5.4). All scenarios in which thresholds were estimated iteratively during simulations (except May's method with 0 measurement error) had lower percentages of years without fishing and higher coefficients of variation of spawning biomass than those under the scenarios with fixed threshold levels. In other words, if the fixed thresholds were true, threshold levels were often underestimated during simulations.

Trends and qualitative results by different threshold estimation methods for EBS herring were similar to those for pollock (Figure 5.4). But benefits with a threshold policy were less for herring than for pollock. The standard deviations of yield, percentages of years without fishing, and coefficients of variation of spawning biomass were much higher for herring. The increase of average yield with a threshold was accompanied with a large increase of standard deviation of yield and percentage of years without fishing. Nevertheless, spawning biomass was much more stable when a high threshold level was used. The influence of measurement error was less important for herring than for pollock. Fowler's rule had a relatively high average yield, low standard deviation of yield, and small chance of closing a fishery. May's method over-estimated the threshold level.

Optimum Threshold Levels

The objective function was used to rank the threshold estimation methods. The top ten methods or levels are illustrated in Figure 5.5 with three levels of measurement error and three weighting factors. There were some decreases in objective function values with estimation error in thresholds. These decreases were less when weighing the standard deviation more heavily. As expected from the results in Chapters 3 and 4, heavier weight put on the standard deviation of yield resulted in smaller optimum threshold levels. Measurement error reduced the value of the objective function and the optimum threshold levels. These results were expected because measurement error greatly reduced the justifiable fishing opportunities, especially with a high threshold level (Figure 5.4). As seen in the previous plots, measurement error also affected the objective functions for pollock more than those for herring. The objective function values of several threshold methods or levels were close to each other, which indicated that the response surfaces were flat.

For EBS pollock, the estimation methods with the best performance were the default 35-50% of pristine biomass and May's method for a weighting factor of 0 (maximum average yield), the default 30-45% of pristine biomass for a weighting factor

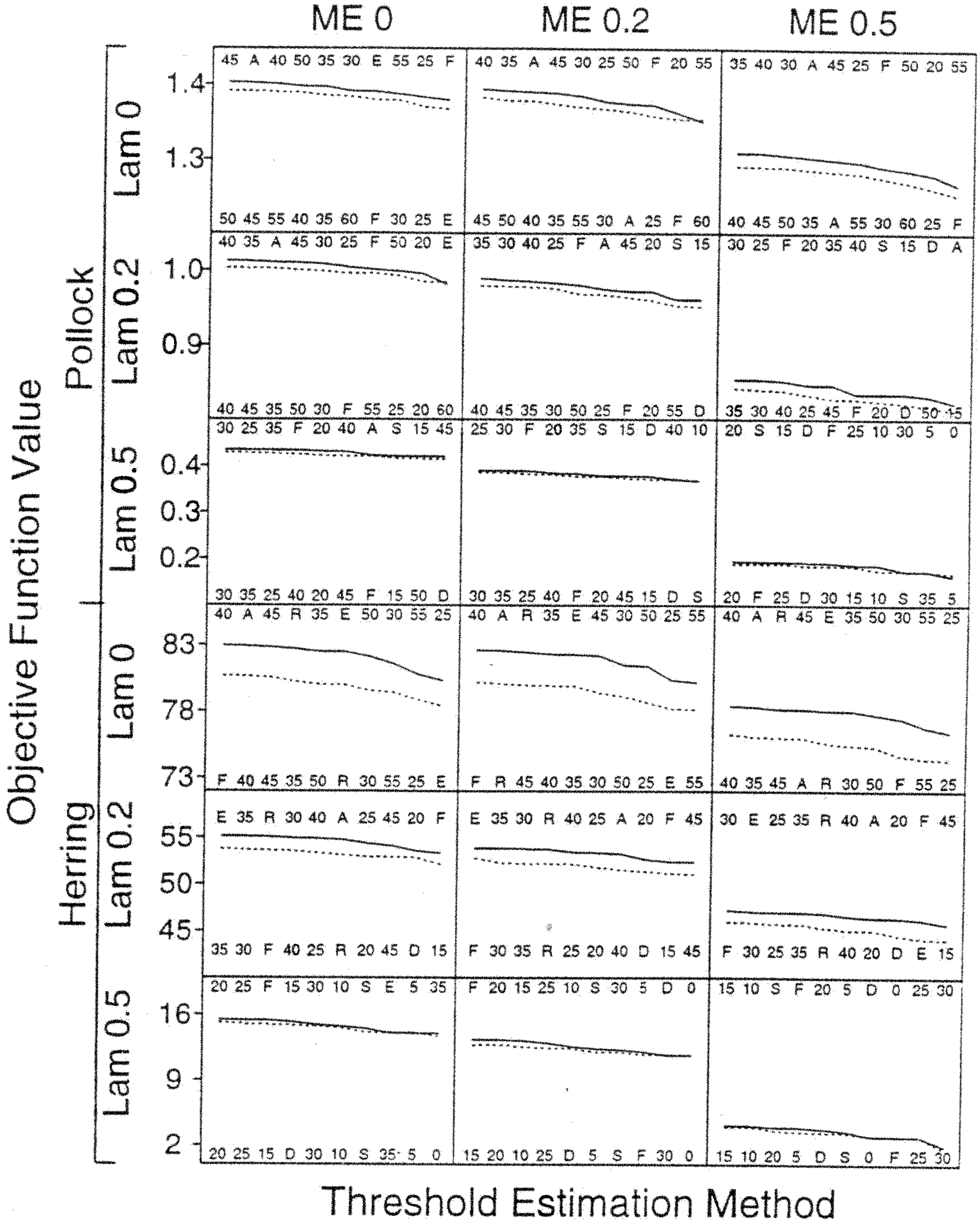

Figure 5.5. The objective function values for the top ten methods (levels) of threshold estimation. The plots are classified by three levels of measurement error (ME), three levels of weighting factor (Lam), and two species (pollock and herring). Implementation error is zero. Solid lines and upper notation are for simulations with fixed thresholds, and dotted lines and bottom notation are for simulations in which thresholds were estimated iteratively. See Table 5.1 for notations of threshold estimation methods.

of 0.2, and the default 20-35% of pristine biomass and Fowler's rule for a weighting factor of 0.5 (equal weighing of average yield and standard deviation of yield; Figure 5.5). Low optimum threshold levels are associated with high measurement errors.

Herring had slightly lower optimum threshold levels than pollock. For EBS herring with the maximum yield criterion, the best methods were the default 35-40% of pristine biomass and spawning biomass per recruit method (Figure 5.5). The performance of Fowler's rule was very good when estimating the threshold but just average using the fixed threshold. In contrast, the performance of May's method was very good with respect to the fixed threshold value but very poor when estimating thresholds. With a weighting factor of 0.2, the best methods were the default 30-35% of pristine biomass, stock-recruit model and Fowler's rule. With equal trade-off criterion, the default 10-25% of pristine biomass and Fowler's rule performed better than other methods. Again as with pollock, measurement errors decreased the optimal threshold levels.

Variation of Estimated Thresholds Over Time

To estimate how many years of data are required to reliably estimate thresholds, I constructed simulations to compare estimated thresholds and their standard deviation as the number of years of data increased with different estimation methods. For EBS pollock, estimated thresholds gradually approached the true values, and the standard deviation generally decreased over time with the default percentage method (Figure 5.6). About 15 to 20 years were required to obtain a reliable estimate of thresholds and to stabilize standard deviation, shorter time being associated with higher levels of thresholds. The trends of estimated thresholds and standard deviation over time with the stock-recruit and spawning biomass per recruit methods were similar under measurement errors 0 and 0.2, and standard deviations were extremely high during the first several years. A high level of measurement error caused large overestimation of thresholds with the stock-recruit method and slight underestimation of thresholds with spawning biomass per recruit method. About 15 to 20 years were required to get a close estimate of

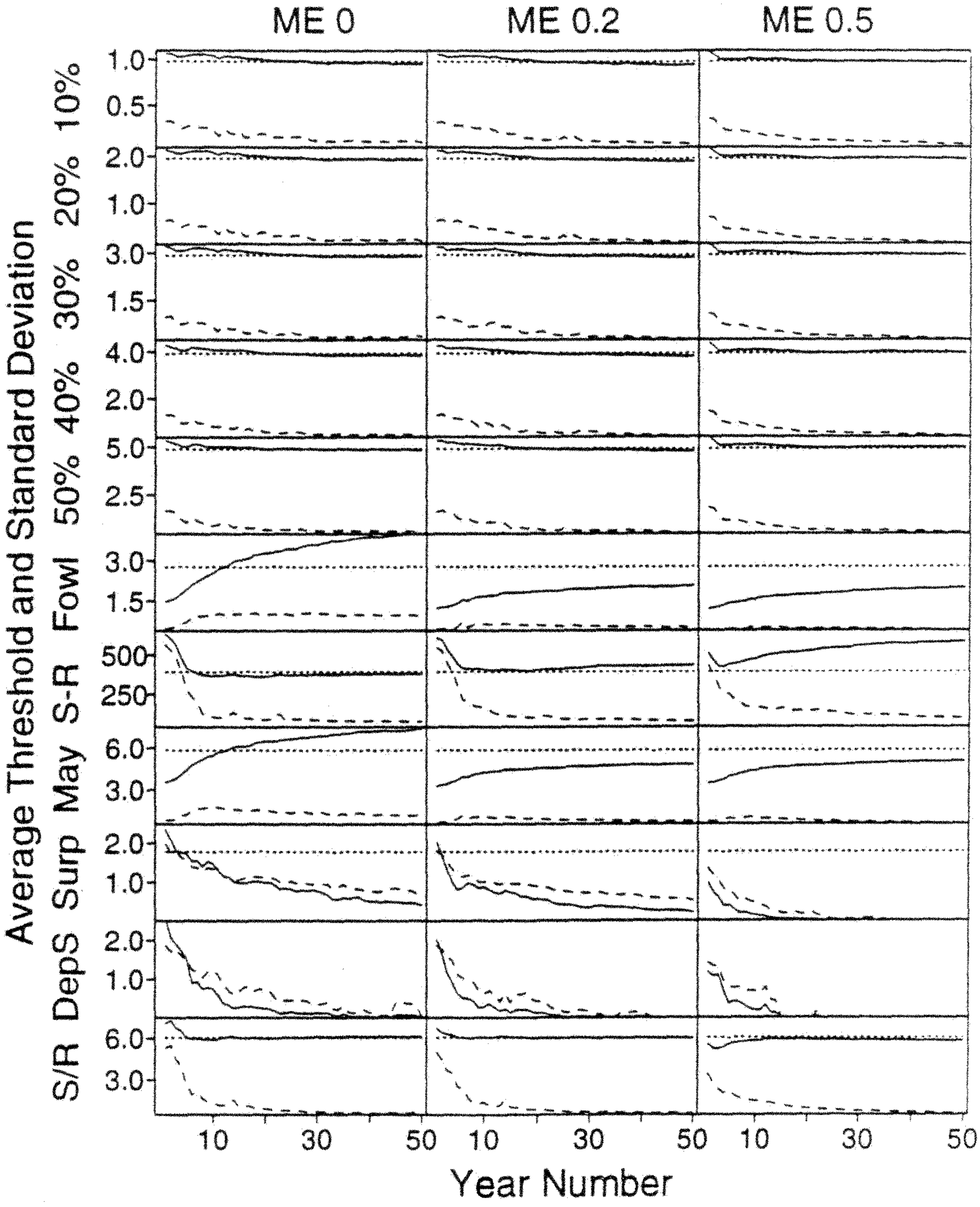

Figure 5.6. Average estimated thresholds and standard deviations over time for eastern Bering Sea pollock by eleven methods (levels) with three levels of measurement error (ME). Implementation error is zero. Solid lines are for average estimated thresholds, dotted lines for true thresholds, and dashed lines for standard deviations of estimated thresholds. Year number 0 corresponds to year 5, i.e., only 5-yr data available. See Table 5.1 for notations of threshold estimation methods.

thresholds and to stabilize standard deviations by these two methods (Figure 5.6).

Fowler's rule and May's method exhibited similar patterns and were greatly influenced by measurement error (Figure 5.6). The estimated thresholds by these two methods increased monotonically without measurement error and gradually approached but did not reach the true values with measurement errors 0.2 and 0.5. Measurement error might reduce the influences of environmental errors and time-lag on recruitment and thus result in better estimates of thresholds. Most of the variations of estimated thresholds were attributed to the pristine biomass estimated by the conventional surplus production model. If auxiliary information were available to constrain the estimates of pristine biomass, the estimated thresholds by these two methods might be greatly improved. Estimated thresholds by the surplus production model and depensatory production model were small and continued to decrease over time, and in many cases they eventually approached zero (Figure 5.6).

The estimated thresholds for herring over time were more variable and took a slightly longer time to approach true values than those for pollock (Figure 5.7). These results may mainly be caused by the influence of higher environmental error on herring recruitment. However, the qualitative conclusions for each method were similar for herring and pollock.

DISCUSSION

Biomass-based threshold estimation methods can be separated into two groups. The first group requires a stock-recruit relation and an estimate of pristine biomass from age-structured models. The default percentage and stock-recruit methods belong to this group.

In this study the default percentage method was the most robust and generally outperformed all other methods. Another advantage of the default percentage method is its flexibility: different percentages can be adopted to achieve different management objectives. The default percentage method is also simple and easy to understand. The common default threshold of 25% pristine biomass was among the optimal threshold

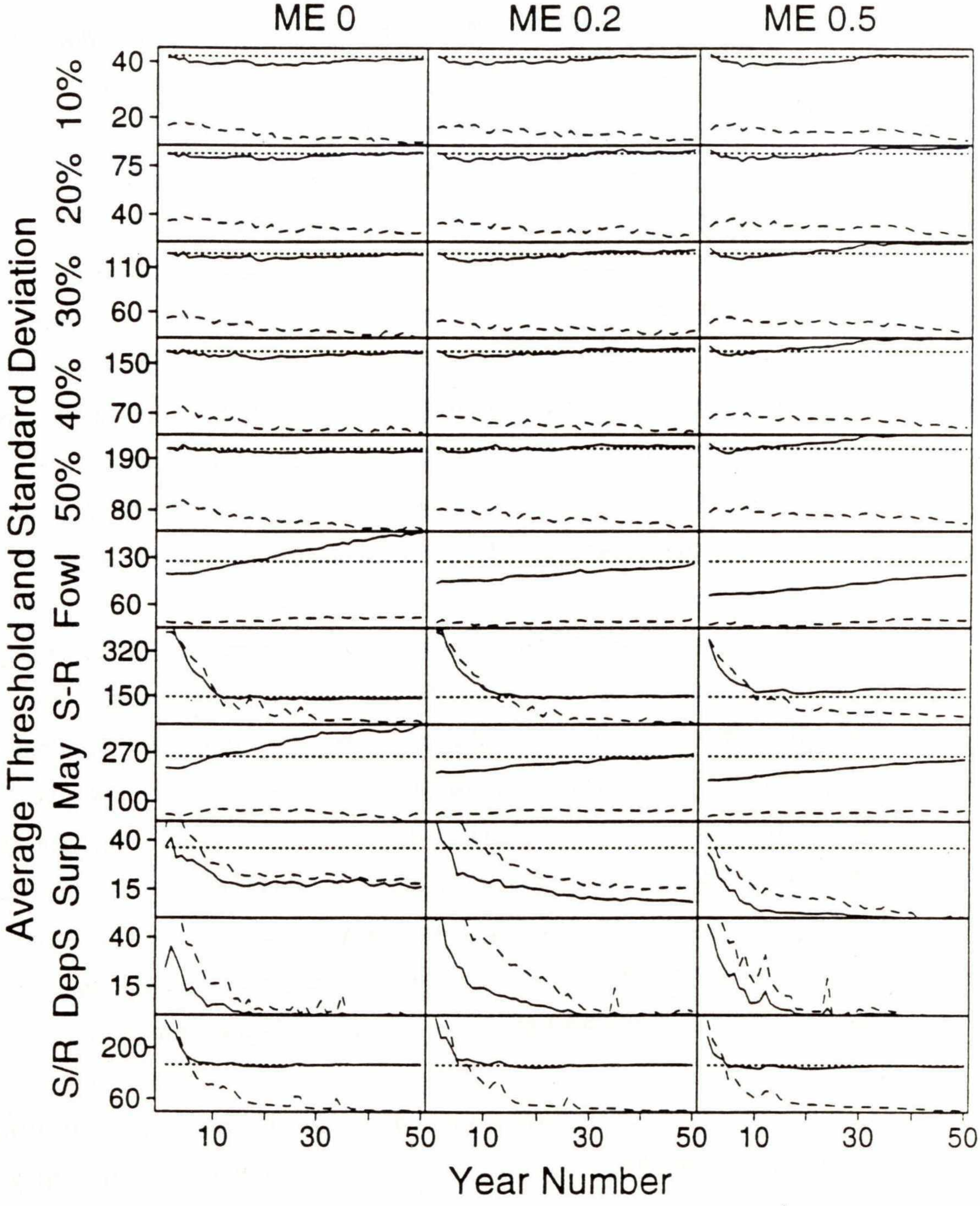

Figure 5.7. Average estimated thresholds and standard deviations over time for eastern Bering Sea herring by eleven methods (levels) with three levels of measurement error (ME). Implementation error is zero. Solid lines are for average estimated thresholds, dotted lines for true thresholds, and dashed lines for standard deviations of estimated thresholds. Year number 0 corresponds to year 5, i.e., only 5-yr data available. See Table 5.1 for notations of threshold estimation methods.

levels when the increase in mean yield and the decrease in standard deviation of yield were weighed equally. Higher threshold levels were required to maximize mean yield. Estimates of pristine biomass may change over time, and thus the estimates need to be updated each year when new data are available.

Theoretically speaking, the stock-recruit method is the best choice for conserving a stock and maximizing its productivity. But in reality, this method is least reliable due to the fact that the stock-recruit method depends only on α which is very sensitive to environmental noise and measurement error (Walters and Ludwig 1981; Armstrong and Shelton 1988). The thresholds estimated by the stock-recruit method were the most variable in this simulation study. Because fecundity is approximately a linear function of body weight for many marine fish, the default percentage method has a similar function as the stock-recruit method to protect a population and enhance its productivity. Therefore, if a stock-recruit relation is available, the default percentage method is recommended.

The second group of threshold estimation methods includes Fowler's rule, May's method and two production models and requires only time series of biomass or catch/effort data. Pristine biomass and threshold level are estimated through production models. Fowler's rule normally provided threshold levels of 15-25% of pristine biomass and performed very well when standard deviations of yield were weighted heavily. May's method estimated a biomass reference point associated with MSY (B_{MSY}) and was favored when the objective function was to maximize yield. Although highly simplified parameters were used in May's model to describe consumer-resource relations, it is difficult to find a marine fish population in which these parameters can be estimated directly.

Because the simulated age-structured models did not contain a depensatory mechanism, I was unable to completely evaluate surplus production and depensatory production models. The majority of estimated thresholds by surplus production and depensatory production models in this study were zero or negative. Actual data for EBS pollock and herring provide estimates of threshold levels of about 10% or less of pristine biomass for these two methods (Quinn and Collie 1990). Unless a given population has a strong depensatory mechanism, surplus production and depensatory production models may not be useful for estimating threshold levels.

The estimation methods of the second group were generally outperformed by the default percentage method of the first group. Furthermore, as Hilborn (1979) observed, catch/effort data alone often failed to estimate the parameters of production models, or generated estimates too far away from the true values. In the case that data are too limited to apply the default percentage method, Fowler's rule gives quite robust results if auxiliary data are available to constrain the pristine biomass estimated by production models.

If only life history parameters are available, it is difficult to estimate biomass-based threshold, but at least one method can be used to estimate a threshold for exploitation rate: spawning biomass per recruit. This method generates exploitation rates that can provide a high yield at low risk (Clark 1991; Sissenwine and Shepherd 1987; Thompson *in press*). The exploitation rates estimated by the spawning biomass per recruit method were converted to spawning biomass thresholds using stock-recruit relations in this study. Most of the variation of estimated thresholds by this method were attributed to the variation of stock-recruit relations. The performance of this method was generally not as good as that of the stock-recruit model.

Environmental factors are believed to influence the recruitment of EBS herring much more strongly than the pollock population. As a result, the estimated thresholds were much more variable, and reliable estimates of thresholds and a stable standard deviation required longer time series of data for herring than for pollock. The optimal threshold levels for herring were generally about 5% less than those for pollock.

The response surfaces of the objective function were flat across threshold estimation methods, and the top five threshold levels (or methods) produced very close objective function values. Thus, threshold management strategies are flexible and a small error in estimation of threshold will not affect the return very much. The loss in objective function values due to estimation error was less than 10% for herring and less than 5% for pollock and smaller with a larger penalty weighting factor.

Because the purpose of this study is to compare different threshold estimation methods with the same set of population parameters, F_{MSY} was assumed known during the simulations. In reality, F_{MSY} is not known for many fish populations and has to be adaptively estimated. If thresholds and F_{MSY} are simultaneously estimated during simulations, the performance of a threshold estimation method may be affected by the estimated F_{MSY}. The bias of estimated F_{MSY} and threshold level is likely be at the same direction (i.e., overestimate or underestimate both F_{MSY} and threshold level at the same time), and thus a portion of the bias may be canceled out.

Actively adaptive management perturbs a population deliberately to provide information to improve estimates of population parameters, especially the stock-recruit relationship (Walters 1986). More accurate population parameters will improve the precision of threshold estimates. In rare cases when a "backup" population is available to enhance the collapsed stock, a population may be used for experimentation to study its dynamics at low biomass levels. Although actively adaptive management benefits threshold management strategies, the gain by adaptive management may be minor because the loss due to estimation errors is small.

Chapter Six

FACTORS AFFECTING OPTIMAL THRESHOLD LEVELS FOR EASTERN BERING SEA HERRING

SUMMARY

Computer simulations were conducted to examine the effects of stock-recruitment relationships, environmental conditions, management objectives and errors, mortalities and other factors on optimal threshold levels for eastern Bering Sea (EBS) herring. A standard set of model parameter values was used for all simulations in which the examined factors were varied over plausible ranges of values. The form of the stock-recruitment (S-R) curve, exploitation rate, and management objective are the three most important factors affecting optimal thresholds. A second group of important factors includes environmental cycle, environmental variation, S-R α, planning horizon, density-dependent natural mortality and measurement error. Environmental autocorrelation and natural mortality patterns are relatively unimportant factors. S-R β, initial biomass and implementation error are unimportant. Optimal thresholds are insensitive to all but the most extreme environmental conditions.

INTRODUCTION

Threshold management strategies aim to protect fisheries resources and enhance long-term productivity of fish stocks. Computer simulations on EBS pollock, *Theragra chalcogramma*, and Pacific herring, *Clupea pallasi*, demonstrated that threshold management policy generally increases average yield and rebuilds overexploited stocks much more quickly than a constant harvest rate policy (Chapters 3 and 4; Quinn et al. 1990; Zheng et al. *in press* a). A threshold management policy also increases management flexibility by furnishing an alternative method to reduce fishing efforts. For some fisheries involving many interest groups, temporarily banning fishing to protect fish stocks may be more acceptable than reducing high fishing efforts (Jakobsson 1985).

Optimal thresholds are population levels or indices which result in the best trade-off between preserving population reproductive potential for the future recruitment and obtaining current yields under a given management objective. If recruitment is density-dependent for a stock, this trade-off is apparent. In cases in which recruitment is regulated by environmental forces, it is also necessary to maintain a minimum level of spawning stock to keep the stock from extinction or falling below a low population level before favorable environmental conditions occur (Sigler and Fujioka *in press*). Several methods have been developed to estimate optimal threshold levels, and computer simulation studies suggested that the default percentage of pristine biomass method usually outperforms other methods (Chapter 5: Zheng et al. *in press* b).

Optimal threshold levels are not only influenced by management objectives and population characteristics, but also by environmental conditions. Computer simulation studies indicate that the management objective, the stock-recruitment relationship, and harvest rate are among the most important factors affecting optimal threshold levels (Quinn et al. 1990; Zheng et al. *in press* a). Although previous simulation studies were able to identify the important factors which affect the optimal threshold levels, the relationships between these factors and the optimal threshold levels are not clear. This chapter extends the previous computer simulations to allow a comprehensive study of the robustness of optimal threshold levels as several factors varied concurrently. For each factor, the likely range of values was divided into small grids (or intervals). An optimal threshold level was estimated for each grid point of these value ranges through computer simulations.

METHODS

Data and Population Models

Preliminary simulations indicated that the effects of several factors on optimal thresholds are qualitatively similar for both EBS pollock and herring, so comprehensive simulations would be conducted only for EBS herring and reported here. Zheng et al.

(*in press* a) conducted cohort-analysis tuned with survey information for EBS herring and summarized the population parameters.

As with previous simulation studies, a typical age-structured single-species model was used in this study. EBS herring are primarily exploited during the sac roe fishery in the late spring or early summer and other fisheries are insignificant. So, I modelled only the sac roe fishery. In the spring each year before spawning, the mature herring biomass B_t was obtained as

(6.1) $B_t = \Sigma_a[N_{t,a} \ m_a \ w_a]$,

where $N_{t,a}$ is abundance just before spawning in year t and at age a, m_a is maturity rate and w_a is weight at age a, which is determined by a general von Bertalanffy growth equation

(6.2) $w_a = W_\infty (1 - \exp[-k(a-t_o)])^b$,

where W_∞, k, t_o and b are growth parameters.

Total yield Y_t was determined as

(6.3) $Y_t = B_t \ h_t$,

where h_t is exploitation rate in year t. To convert the yield to catch in number by age, I estimated exploitable biomass EB_t as

(6.4) $EB_t = \Sigma_a[N_{t,a} \ s_a \ w_a]$,

where s_a is gear selectivity coefficient by age. The effective exploitation rate by age is

(6.5) $H_{t,a} = h_t \ s_a \ B_t/EB_t$.

The catch (in number) was calculated as

(6.6) $C_{t,a} = N_{t,a} \ H_{t,a}$.

Total spawning biomass, S_t, was

(6.7) $S_t = \Sigma_a[(N_{t,a} - C_{t,a}) \ w_a \ m_a]$.

The abundance was advanced to the next year, $N_{t+1,a+1}$, as

(6.8) $N_{t+1,a+1} = (N_{t,a} - C_{t,a}) \exp(-M_a)$

for all ages except the oldest age in the model and by

(6.9) $N_{t+1,la} = (N_{t,la-1}-C_{t,la-1})\exp(-M_{la-1})+(N_{t,la}-C_{t,la})\exp(-M_{la})$ for the maximum age (la)

in the model.

A general model was used to describe the stock-recruit relationship because of flexibility (Deriso 1980):

(6.10) $N_{t,r} = \alpha\, S_{t-r}\, [1 - \beta\, \gamma\, S_{t-r}]^{1/\gamma} \exp(v_t)$,

where r is the recruiting age, α, β and γ are parameters, and v_t is a random variable representing influences of environmental factors on recruitment.

Simulations

Fifteen factors were examined in the simulations and each factor was evaluated for at least 10 grid points within the most likely data range. The data range for each factor was summarized in Table 6.1. These factors include 3 parameters from the stock-recruitment model, exploitation rate, natural mortality pattern, density-dependent mortality, environmental variation, autocorrelation and cycle, measurement and implementation errors, initial biomass and planning horizon.

Ten hypothetical instantaneous natural mortality patterns are shown in Figure 6.1. The overall natural mortalities of the whole population are basically the same among these ten patterns. The difference among the patterns is mortality by age. The highest mortality occurs in youngest and oldest fish with patterns 1 and 10, respectively.

Density-dependent natural mortality on herring was proposed by Haist et al. (*in press*). The instantaneous natural mortality in year t is

(6.11) $M_t = [m_0 + \exp(-d\, B_t/B_\infty)]/G$,

where m_0, d and G are constants, and B_∞ is the pristine biomass. m_0 was approximately set to 0.2, based on the results by Haist et al. (*in press*) and G was adjusted such that M_t would be 0.35 (the average natural mortality) if the population biomass was equal to the biomass associated with maximum sustained yield (MSY). Parameter d was varied to examine the density-dependent effects.

Many environmental factors fluctuate with a long-term, periodic cycle, superimposed by random noises (Koslow 1989; Hollowed 1990). A convenient way to model this phenomena is by a sine function:

Table 6.1. Summary of ranges of factors examined for their influences on optimal threshold levels. If two or more increments were used for a factor, smaller increments were generally used for the lower end of the data range.

Factor	Value Range			Grid Point #	Increment
Penalty Weighting Factor	0.0	to	1.0	11	0.1
S-R α	1.0	to	20.0	16	0.5, 1.0, 2.0
S-R β	0.001	to	0.016	16	0.001
S-R γ	-2.0	to	0.4	16	0.1, 0.2
Exploitation Rate	0.1	to	0.6	16	0.025, 0.05
M Pattern	1.	to	10.	10	1
D-D Mortality (d)	-2.0	to	5.5	16	0.5
Environ. Variation (σ)	0.0	to	2.0	16	0.15, 0.2
Environ. Autocorrelation	-0.95	to	0.95	16	0.1, 0.15
Cycle Amplitude (A)	0.0	to	5.0	11	0.5
Cycle Period (κ,in Yr)	0.	to	30.	11	3
Measurement Error	0.0	to	1.0	11	0.1
Implementation Error	0.0	to	1.0	11	0.1
Initial Biomass	5%	to	60%	16	2.5%, 5%
Planning Horizon (Yr)	5.	to	100	16	5, 10

Abbreviations:
S-R: stock-recruitment model
M: instantaneous natural mortality
D-D: density-dependent.

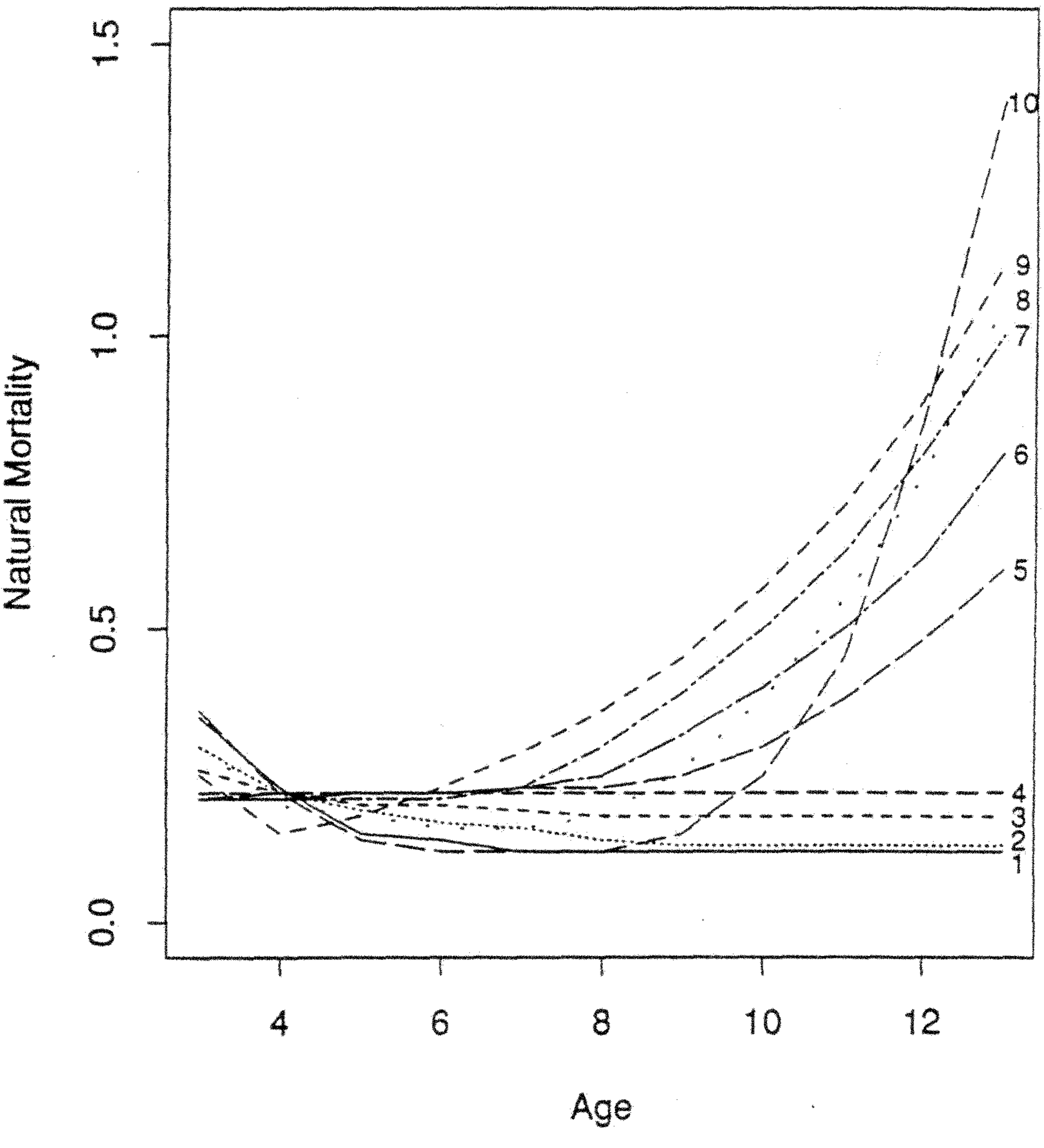

Figure 6.1. Ten alternative instantaneous natural mortality patterns by age for eastern Bering Sea herring.

(6.12) $v_t = A \sin(t\, 2\pi/\kappa + s) + v'_t$,

where A is amplitude, κ period, and s a phase determined randomly for each replicate. During the simulations A and κ were varied to examine their effects on optimal threshold levels. An adjusted constant C was added to equation (6.12) such that the expected value of $\exp(A \sin(t\, 2\pi/\kappa + s))/C$ was equal to 1 to correct the skewed effects of high A values. v'_t is a random variable assumed to follow a normal distribution with mean 0 and variance σ^2 (Quinn et al. 1990).

Different values of a factor may result in different pristine biomasses and optimal exploitation rates, which will affect the optimal threshold levels. To minimize the influences of pristine biomass and exploitation rate, the threshold levels were expressed as percentage of pristine biomass, and exploitation rate associated with MSY was used in simulations for each grid of each factor. An exception was made in simulations for examining the exploitation rate factor, in which different levels of exploitation rates were used. For each grid of a factor, an age-structured model was iterated for 300 years with expected effects of environmental noises on recruitment, and the statistics from the last 200 years were averaged. The average biomass without exploitation was used as pristine biomass, and the exploitation rate that produced the highest average yield was termed the exploitation rate associated with MSY.

To compare all factors on a common standard, all simulations were carried out with a standard set of parameters except the values of the factor examined. The standard population parameters were those estimated for EBS herring. Measurement error, implementation error, and environmental autocorrelation were all assumed not to occur. The planning horizon was 50 years and initial biomass was 15% of the pristine level. Because I am interested only in comparing optimal thresholds for different values of the examined factors under a given environmental condition in this Chapter, 101 replicates were adopted and an identical set of numbers was used as seeds for random number generator for all factors.

Optimal Criteria

The objective function to evaluate optimal threshold levels is the trade-off between increased average yield and decreased variation in yield. Detailed descriptions of this objective function are given by Quinn et al. (1990) and Zheng et al. (*in press* a). The function is a linear combination of average yield and the standard deviation of yield over the planning horizon, or

(6.13) $\max\ [(1 - \lambda)\ Y_{th} - \lambda\ SD_{th}]$,

where Y_{th} and SD_{th} are average annual yield and standard deviation under threshold level "*th*", and λ is a penalty weighting factor. There are three special cases: maximum average yield (λ=0), equal trade-off of increased average yield with decreased standard deviation (λ=0.5), and minimum variation in yield (λ=1.0).

RESULTS

Stock-recruitment Relationship

The relationships among optimal threshold levels, the penalty weighting factor and three parameters of the general stock-recruitment curve are shown in Figure 6.2. Each plot in Figure 6.2 consists of three planes: XY, XZ and YZ. The XY plane is contours of optimal threshold levels, the XZ plane shows the relationship between weighting factor and optimal thresholds, and the YZ plane illustrates the general trend of optimal thresholds versus the three S-R parameters. The dots in the XZ and YZ planes are estimated optimal threshold levels for all values of the XY grid, and the solid lines are LOWESS smoothing curves (Becker et al. 1988) over the estimated optimal threshold levels. The common feature for three parameters was that optimal thresholds were negatively associated with weighting factor: the heavier the variation in yield is weighed, the smaller the optimal thresholds. If the objective function was to minimize the variation in yield, then no threshold should be applied.

Parameter γ represents the form of the stock-recruitment curve and was the most important factor to affect optimal threshold levels (Figure 6.2). A smaller γ results in less density-dependent recruitment and a dome-shaped stock-recruitment curve occurs

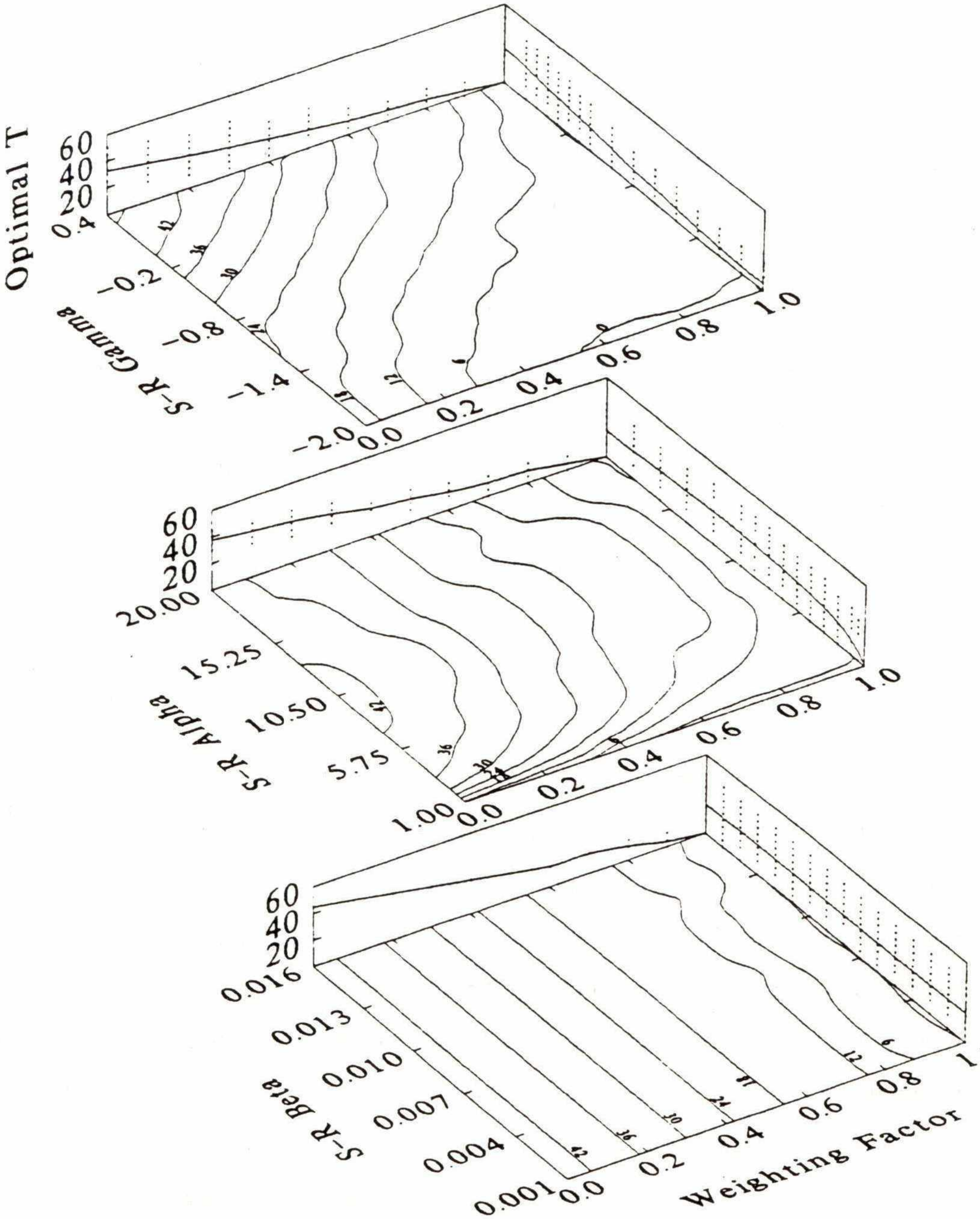

Figure 6.2. Contour plots for the optimal threshold levels (% of pristine biomass) as a function of penalty weighting factor and three parameters of stock-recruitment model.

when $\gamma > -1.0$. For a given weighting factor, higher γ resulted in higher optimal thresholds. When $\gamma < -1.0$, all optimal thresholds were less than 25% of pristine biomass. Optimal threshold levels were much higher with a Ricker stock-recruitment curve ($\gamma = 0$) than with a Beverton-Holt curve ($\gamma = -1$).

Parameter α represents productivity potential or the original slope of the stock-recruitment curve. Optimal threshold levels were very sensitive to low α values which resulted in small optimal threshold levels (Figure 6.2). When α was close to or larger than the estimated values, the optimal thresholds were fairly constant, with higher α values resulting in slightly smaller optimal threshold levels.

As expected, density-dependent parameter β did not affect the optimal threshold levels (Figure 6.2). This is primarily due to the fact that threshold levels are expressed as percentages of pristine biomass. Although β affects both the absolute threshold and pristine biomass, effects of β may have been canceled out after the absolute threshold is divided by the pristine biomass, because β is a scale parameter that alters dimensions of the curve but not its shape.

To illustrate the effects of S-R parameter interactions on optimal threshold levels, I estimated optimal threshold levels through computer simulations under combinations of parameters α and γ. Figure 6.3 shows those optimal thresholds with 3 levels of weighting factors: 0.0, 0.2 and 0.5. As expected, the greatest effects on optimal thresholds resulted from parameter γ. The optimal thresholds were more sensitive to γ with α close to or greater than the estimated level than with α being small. The parameter α affected the optimal threshold levels more strongly with $\gamma > 0.0$ than with other γ values. The patterns of optimal threshold levels among three levels of weighting factors were similar except that higher weighting factors were associated smaller optimal thresholds.

Mortalities

The effects of three kinds of mortalities on optimal thresholds were examined.

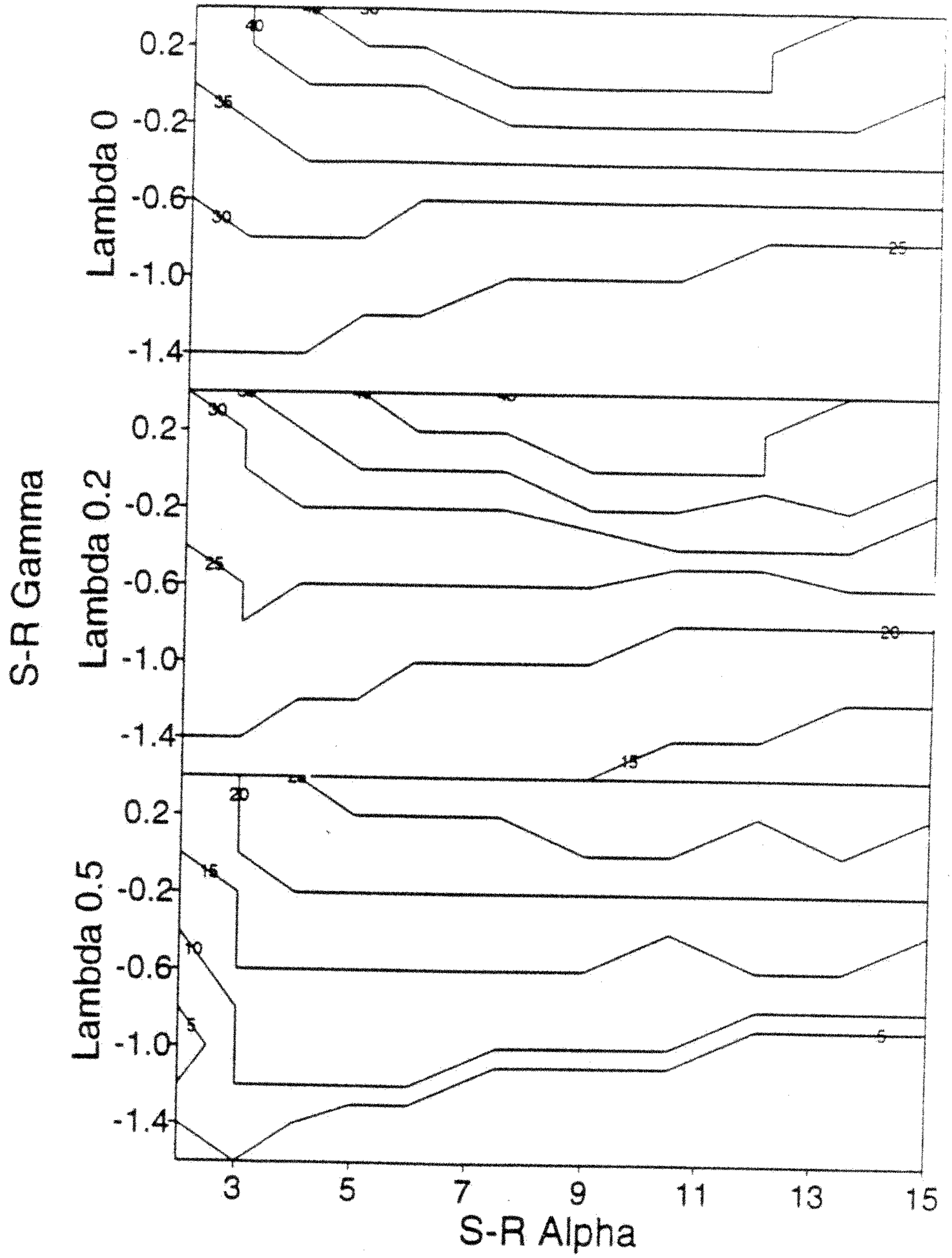

Figure 6.3. Contour plots for the optimal threshold levels (% of pristine biomass) as a function of parameters α and γ of stock-recruitment model with three levels of penalty weighting factor: 0.0, 0.2 and 0.5.

Instantaneous natural mortality pattern (i.e., age-dependent natural mortality) generally had a very minor effect on optimal thresholds (Figure 6.4). Higher natural mortality for younger fish resulted in slightly smaller optimal threshold levels. This supports the results for parameter α (Figure 6.2), because higher mortality for younger fish (recruitment) is one factor that would result in lower productivity (i.e., small α). Different levels of natural mortalities on older fish did not affect optimal thresholds with weighting factors less than 0.5.

The relationships between density-dependent mortality and optimal thresholds were complex. When density-dependence was weak (coefficient d is about from -0.5 to 0.5), the effects of density-dependent mortality on optimal thresholds were minor (Figure 6.4). Optimal threshold levels for a given weighting factor tended to rise with increasing compensatory density-dependent mortalities ($d < 0$). Higher depensatory density-dependent mortalities resulted in much larger optimal threshold levels for weighting factors less than 0.5. This would prevent the stock from reaching low abundance levels. High depensatory density-dependent mortality increased the variation of population abundance and yield. Such high standard deviations of yields resulted in negative objective function values with weighting factors greater than 0.6, so the optimal threshold levels were equal to zero (Figure 6.4).

Exploitation rate was an important factor affecting optimal thresholds. With weighting factors less than 0.5, optimal threshold levels were positively related to exploitation rate (Figure 6.4). When exploitation rate was very low, no threshold was needed. On the other hand, when exploitation rate was very high, a high threshold effectively reduced the fishing mortality, resulting in a pulse fishing scenario in which the highest possible yield could be obtained, but with extremely high variation in yield.

Environmental Noises on Recruitment

First-order environmental autocorrelation was used in this part of the study. Here, negative autocorrelation means a strong year-class tends to follow a weak year-class and vice versa. With positive autocorrelation, a strong-year class tends to follow

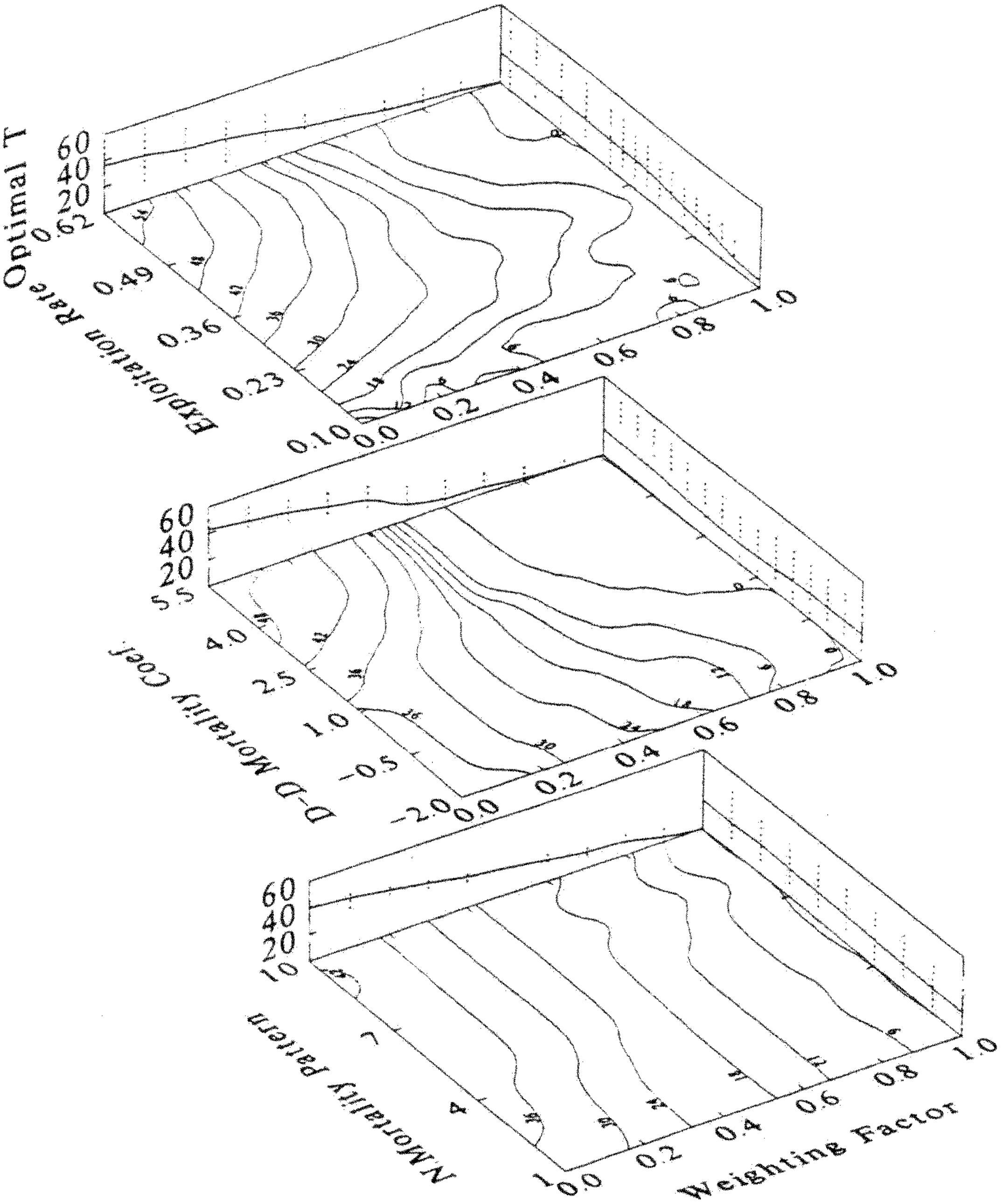

Figure 6.4. Contour plots for the optimal threshold levels (% of pristine biomass) as a function of penalty weighting factor, natural mortality pattern, coefficient of density-dependent natural mortality and exploitation rate.

another strong year-class, and a weak year-class tends to follow another weak one. The simulation results show that with autocorrelation coefficients ranging from -0.5 to 0.5, optimal thresholds were basically independent of environmental autocorrelation (Figure 6.5). With extreme negative autocorrelations, optimal thresholds tended to increase with a given weighting factor. Extreme positive autocorrelations slightly reduced the optimal threshold levels with weighting factor less than 0.3.

Environmental variation (i.e., parameter σ) measures the proportion of recruitment variation caused by environmental forces. When σ was less than 0.4, environmental variation had a very little effect on optimal threshold levels (Figure 6.5). Optimal thresholds slightly decreased with a given weighting factor when σ gradually increased from 0.4 to 1.3, and dramatically decreased when σ is larger than 1.3. It is intuitive that higher environmental variation results in less dependence of recruitment on spawning stocks and more difficulty in maintaining the stock at a desired abundance level, thus reduces optimal threshold levels. The effects of environmental variation on optimal thresholds were much larger with management objectives favoring stable yield than favoring maximum yield (Figure 6.5).

The influences of environmental cycles on optimal thresholds depended on the amplitude and period of cycles and weighting factors (Figure 6.6). With weighting factors ≤ 0.2, optimal thresholds were basically independent of environmental cycles with periods ≤ 8 years and periods from 13 to 30 years with amplitudes < 2.0, and markedly decreased with periods increasing from 8 to 12 years. The average life span of EBS herring is about 8 to 12 years with H_{MSY} exploitation rate. When the period became greater than the herring life span, there was no way to keep the stock above a high threshold, thus optimal thresholds decreased with period length. With a weighting factor equal to 0.5, the equal trade-off between average yield and standard deviation of yield, environmental cycles with periods from 2 to 8 years reduced optimal threshold levels dramatically. Generally speaking, increasing amplitudes of environmental cycles resulted in decreasing optimal threshold levels. The most sensitive effects of amplitudes on optimal thresholds occurred for amplitudes from 1.0 to 2.0. The optimal threshold

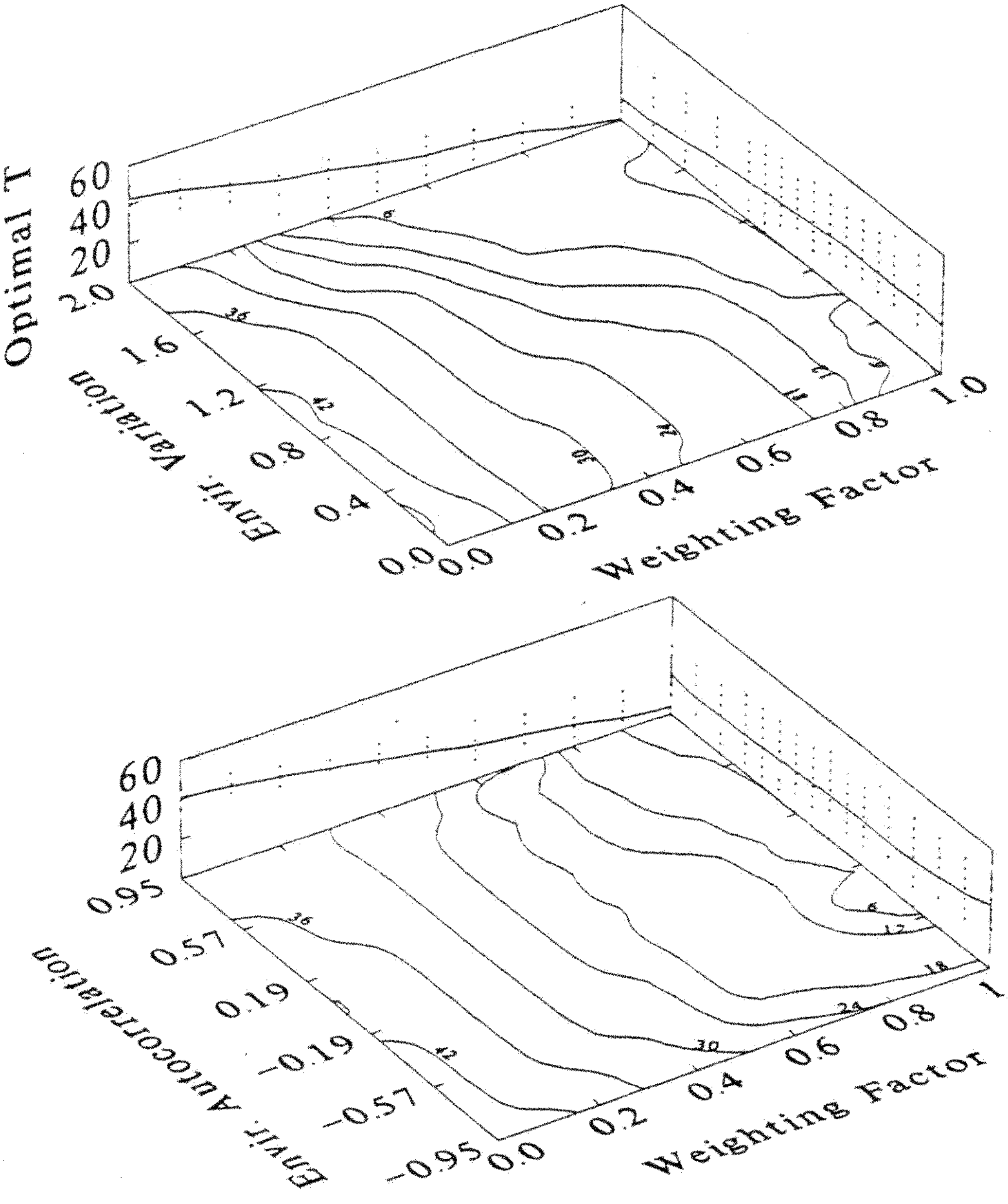

Figure 6.5. Contour plots for the optimal threshold levels (% of pristine biomass) as a function of penalty weighting factor, environmental autocorrelation and environmental variation (σ).

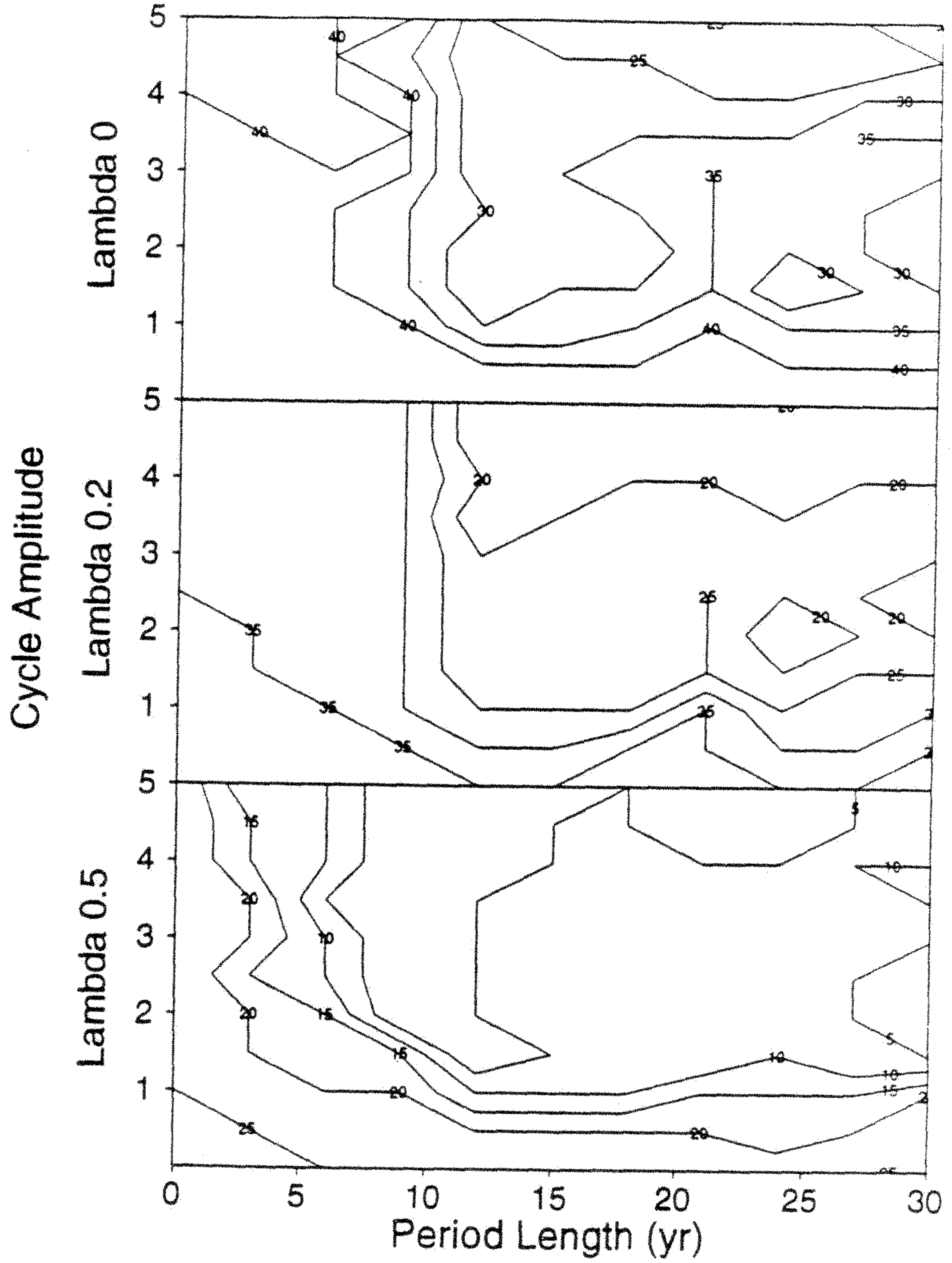

Figure 6.6. Contour plots for the optimal threshold levels (% of pristine biomass) as a function of amplitude and period of environmental cycles with three levels of penalty weighting factor: 0.0, 0.2 and 0.5.

levels with a given period were relatively unrelated to amplitudes of environmental cycles when the amplitudes were greater than 2.0 (Figure 6.6).

Management Errors

In managing a fishery, two kinds of management errors may occur: errors in measuring population abundances (measurement error) and errors in implementing harvest strategies (implementation error). In this study, measurement error was assumed to follow a lognormal distribution and implementation error a normal distribution. To reduce the influences of extreme outliers, I truncated measurement error by 95% confidence intervals and implementation error by 90% confidence intervals.

The contours of optimal threshold levels as a function of measurement and implementation errors are shown in Figure 6.7. Overall, implementation error had a very minor effect on optimal thresholds. When management objectives were to maximize average yield, optimal thresholds were generally independent of measurement error. Extremely high measurement errors slightly increased optimal threshold levels. Under the management objective of equal trade-off between average yield and standard deviation of yield, optimal thresholds were negatively associated with measurement errors, with higher measurement errors resulting in much smaller optimal threshold levels, because the standard deviation of yield increased much more rapidly than the average yield as the threshold level increased.

Other Factors

Initial biomass determines the population status when the simulations start. The simulation results show that optimal thresholds were not related to initial biomass, especially with weighting factors ≤ 0.5 (Figure 6.8).

Planning horizon is the duration in which population and catch statistics are collected in the simulations. A short and a long planning horizon means that the management objectives focus on short-term and long-term benefits, respectively. As expected, a short planning horizon (less than 7 years) resulted in small optimal threshold

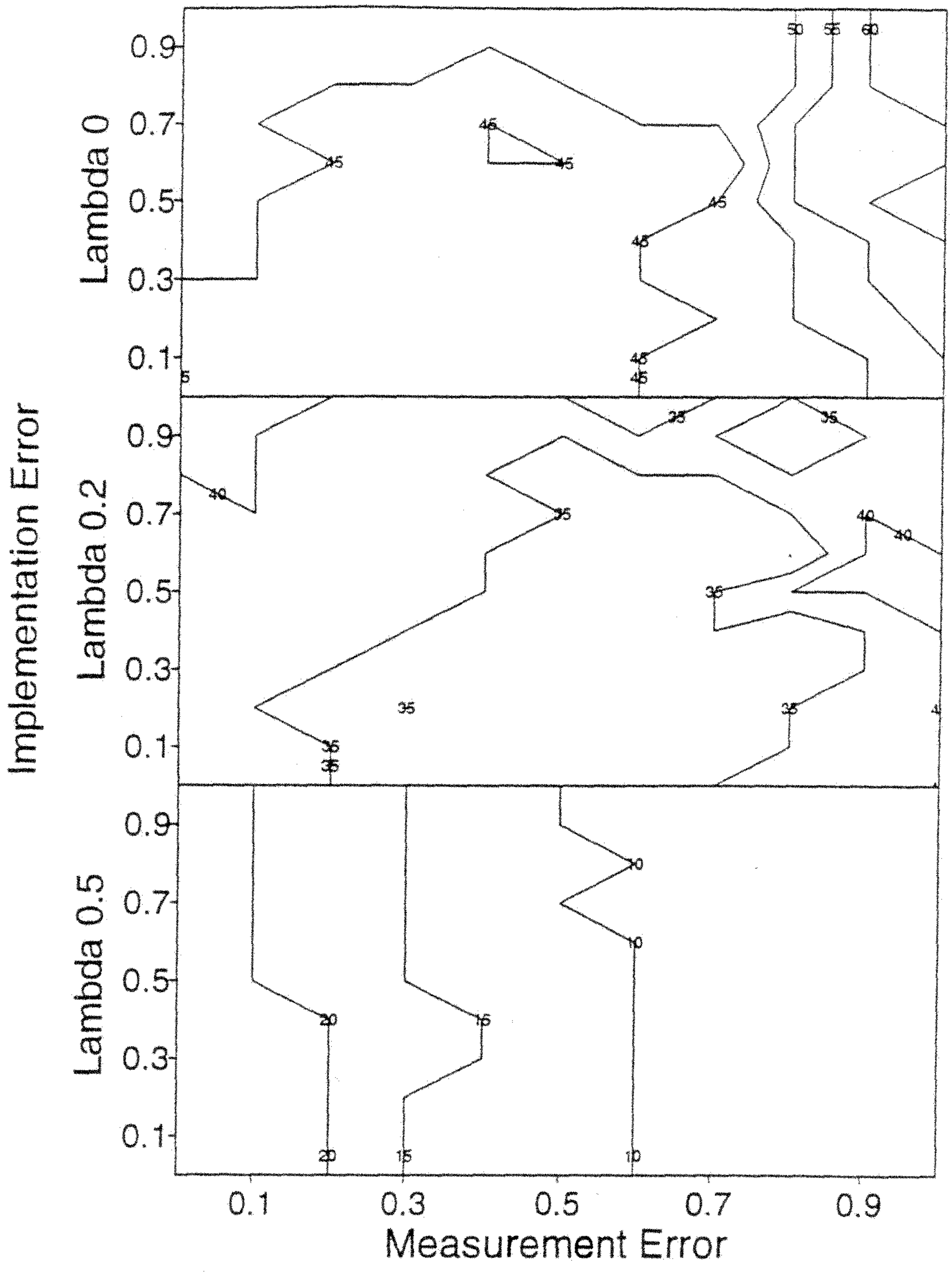

Figure 6.7. Contour plots for the optimal threshold levels (% of pristine biomass) as a function of measurement and implementation errors with three levels of penalty weighting factor: 0.0, 0.2 and 0.5.

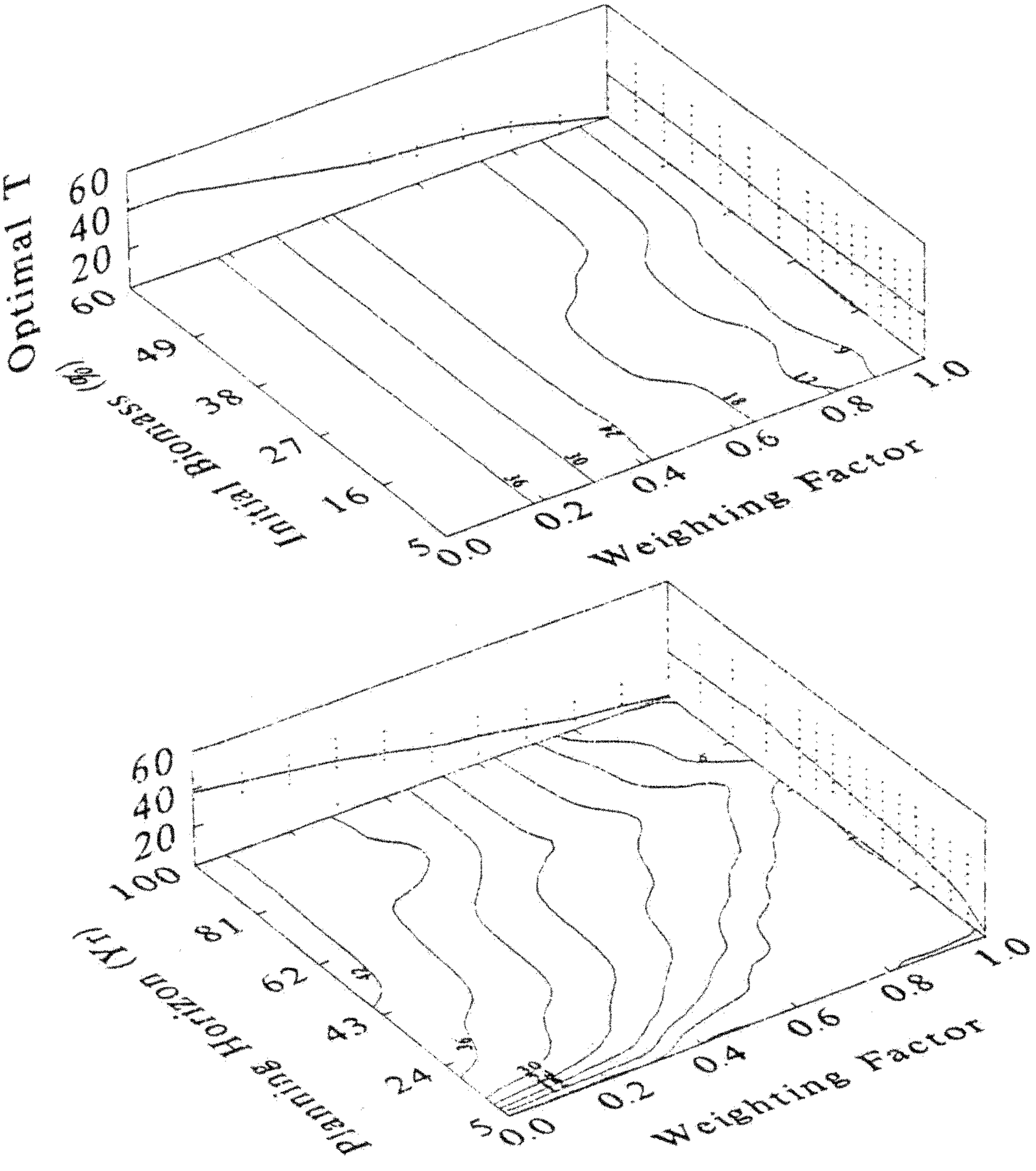

Figure 6.8. Contour plots for the optimal threshold levels (% of pristine biomass) as a function of penalty weighting factor, initial biomass and planning horizon.

levels, or no thresholds at all (Figure 6.8). For a given weighting factor, optimal threshold levels gradually increased with increasing planning horizons from 5 to 30 years. With weighting factors less than 0.5, optimal thresholds were generally constant with planning horizons from 30 to 50 years and slightly increased with planning horizons greater than 50 years. This results occurred because the population was initially rebuilding.

DISCUSSION

Management objectives are one of the most important factors affecting optimal threshold levels. Results in this chapter corroborated the findings in Chapters 3, 4 and 5. The simple objective function includes a variety of management objectives ranging from maximizing average yield, which results in the highest optimal thresholds, to minimizing variation in yield (or obtaining constant yield), which results in no threshold at all. For herring fisheries in Alaska, the management objectives are between maximum average yield and equal trade-off between average yield and variation in yield, so that the resources can be protected and high yield sustained (Zheng et al. *in press* a).

The form of the stock-recruitment curve has major effects on optimal threshold levels. It also plays a major role in determining average yield and exploitation rate. Optimal thresholds with the same management objectives, MSY and fishing mortality associated with MSY are larger with a Ricker model than a Beverton-Holt model for EBS pollock (Quinn et al. 1990). For the three stocks examined in this study, the highest optimal thresholds were found for EBS pollock with the most dome-shaped stock-recruitment curve and the lowest optimal thresholds were obtained for PWS herring with the least dome-shaped curve. Smaller γ results in a lower percentage of pristine biomass and exploitation rate associated with MSY, which partially explains the smaller optimal threshold levels and MSY. Optimal thresholds are generally less or equal to the percentage of pristine biomass producing MSY. Another important factor contributing to the smaller optimal threshold levels is that with smaller γ the recruitment is less density-dependent on spawning stocks. The benefits of enhancing the reproductive potential and long-term yield by fishery closure are smaller with less density-dependent recruitment unless the spawning stock is very low.

Cushing and Harris (1973) showed that the forms of stock-recruitment curves were strongly dome-shaped for the gadoid stocks (high γ), dome-shaped for the salmon stocks, and flat for the flatfish stocks (low γ). Thus, higher optimal thresholds may be needed and larger benefits may be realized from a threshold approach for the gadoid and salmon stocks than for the flatfish stocks. But we must be cautious in generalizing the form of stock-recruitment curves for a large group of fish stocks. For example, Koslow et al. (1987) concluded that the recruitment is independent of spawning stock for both Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) stocks in the northwest Atlantic. Chapter 2 showed that although many herring stocks exhibit dome-shaped stock-recruitment curves, no stock-recruitment relationships can be found for some other herring stocks.

The relationship between productivity parameter α and the optimal threshold levels is somewhat more complex, and for a given management objective the highest optimal thresholds occur with intermediate α. Lower productivity for a stock provides less incentive to close fishing when stock abundances are relatively high because the loss due to natural mortality outweighs the gain of future recruitment, and thus results in smaller optimal thresholds. On the other hand, higher productivity means the recruitment is less dependent on spawning biomass, thus the optimal thresholds are smaller. Although density-dependent parameter β is the most important factor determining the optimal escapement goal for many fish stocks, its effects on optimal thresholds are canceled out after expressing the threshold levels as a percentage of pristine biomass.

Exploitation rate is positively associated with optimal thresholds for the management objective of maximum yield. This suggests the maximum yield for a population may be realized by different harvest strategies with a similar level of exploitation. Getz et al. (1987) reached similar conclusions for three different stocks. The level of exploitation can be a constant exploitation rate, or a combination of exploitation rates and thresholds. The advantages of the threshold approach are to increase management flexibility and robustness, at least theoretically. The response surface of yield is much flatter with a threshold approach than with an exploitation rate approach alone, and a yield close to the maximum yield could be produced under many combinations of exploitation rates and thresholds (Quinn et al. 1990; Zheng et al. *in press* a). In addition, a threshold approach will prevent overfishing and protect the reproductive potential when exploitation rate is high. Furthermore, when a population is overexploited, a threshold approach will rebuild the population much more quickly than an exploitation rate approach alone (Chapters 3 and 4; Quinn et al. 1990).

Optimal thresholds are not strongly influenced by density-dependent natural mortality unless such mortality is very high. Highly density-dependent natural mortality results in much higher optimal threshold levels than those under a constant natural mortality. In simulation studies on herring fisheries in British Columbia, Haist et al. (*in press*) showed that depensatory natural mortality not only reduces the exploitation rate associated with MSY, but also increases the chance of stock collapse. Their results suggest that a threshold is needed for such a population to prevent population collapse. Similar results were obtained from a surplus production model with depensatory natural mortality and autocorrelated environmental noise for Sitka Sound herring (Collie and Spencer *in press*). The likely mechanisms to cause density-dependent natural mortality are predation and competition. When the population abundance is low, predation may remove a higher proportion of the population, which results in depensatory natural mortality. On the other hand, when the population abundance is high, competition for food and space, or easily spreading contagious diseases could lead to compensatory natural mortality. Therefore, when the effects of species interactions are taken into account, a higher threshold may be required to protect the population and meet management objectives.

The effects of environmental factors on optimal thresholds are manifested through their influences on recruitment. When recruitment variation is primarily caused by environmental forces, there is less incentive to preserve current spawning stocks to ensure future recruitment. Thus, optimal threshold levels are much higher without environmental effects than with strong environmental influences. Environmental variation (parameter σ) accounts for random environmental conditions and is less than 1.2 for a variety of commercially important populations around the world (Hightower and Grossman 1985). Values in this range have only minor influences on optimal threshold levels. Environmental autocorrelations for herring generally involve a time lag of 1 or 2 years with an autocorrelation coefficient less than 0.5 (Chapter 2), so their effects on optimal thresholds are negligible. The most important effects of environmental conditions on optimal thresholds are caused by low-frequency and high-amplitude cycles. Such strong cycles, if they exist, primarily control recruitment success and can keep the population low for a long period of time; thus the optimal thresholds are small. Nevertheless, in this case the threshold approach still outperforms non-threshold approaches because a threshold is still needed to minimize the risk of population collapse. For such environmental conditions, two levels of thresholds may be more appropriate: a high level for favorable environmental conditions and a low level for unfavorable environmental conditions. In examining the population dynamics under the environmental cycle, Parma (1990) concluded that the optimal management strategy for maximizing expected discounted yield is to raise escapements when favorable environmental conditions are anticipated and to lower escapements when poor environmental conditions are expected. However, the optimal time-dependent feedback strategy for maximizing expected sum of discounted logarithms of catches closely resembles a constant harvest rate strategy (Parma 1990). Although many populations have been documented with low-frequency and high-amplitude cycles (Cushing 1982; Koslow et al. 1987; Koslow 1989), recruitment time series for many populations are too short to offer compelling evidence for such cycles.

For stocks with cyclic, periodic recruitment, the threshold approach works like a "banking policy": to protect the capital for future returns. The "banking policy" works only if two assumptions are valid: 1) a certain level of spawning stocks is needed to produce average or strong year-classes; 2) the mean lifespan of a stock is longer than the unfavorable period of environmental cycles. The optimal threshold levels are the trade-off among the mean lifespan of the stock, the period length of environmental cycles and the productivity of the stock. The "banking policy" may be attractive to a long-lived species because of the long lifespan.

Because threshold management strategies aim to enhance the well-being of populations and yields over the long term, the planning horizon should be long-term. A long-term planning horizon generally does not significantly influence optimal threshold levels.

Initial biomass represents the initial status of the stock when simulations start. A low initial biomass means the stock has been overexploited and needs to rebuild. Although the results in this Chapter suggest that optimal thresholds are insensitive to initial biomass, the gain in average yield from a threshold approach over a non-threshold approach is greater with a low initial biomass than with a high initial biomass (Chapters 3 and 4). If an initial biomass equal to or greater than the biomass at MSY and a low or intermediate exploitation rate are used, and if the simulated population always stays at about the equilibrium level, a threshold approach will be identical with a constant harvest rate approach, because the population does not fall below any threshold levels. But for a long horizon, say 50 years, it is rare to find any exploited populations which abundances always are at equilibrium levels, or equal to or greater than the abundances at MSY. Besides enhancing long-term yield, a threshold approach can also reduce the risk of population collapse (Single and Fujioka *in press*). Furthermore, once a population collapses, the population will rebuild more quickly with threshold management strategies than non-threshold strategies.

A low initial biomass puts the population below many threshold levels and performance of different threshold levels can be evaluated. Alternatively, the causes for population collapse are built in the simulations to evaluate the threshold approach (e.g., Collie and Spencer *in press*). The likely causes for population collapse are high fishing mortality, suddenly increase of natural mortality and continuous failure of recruitment. It is a challenge to build a simulation incorporating all these causes for a specific population, because it is difficult to model variation in natural mortality over time and the causes of recruitment failure. Using a low initial biomass is a simple way to avoid modelling the causes for population collapse. Some computer simulations (e.g., Hollowed and Megrey *in press*) neither started from a low initial biomass, nor incorporated the causes for population collapse. It is not surprising that the results from such simulation studies suggest that a threshold approach is useless, because the simulated populations hardly dropped below a threshold level. The threshold approach primarily deals with the population dynamics at low population abundance levels. Simulation studies without incorporating low population abundances cannot be used to evaluate the threshold approach.

The simulation results show that random management errors (measurement and implementation errors) have minor effects on optimal threshold levels unless the weighting factor is very high, but nonrandom management errors could occur for a fishery (Zheng et al. *in press* a). The effects of systematic, nonrandom management errors on optimal thresholds are likely similar to those of exploitation rate. Systematically overestimating or underestimating population abundances, or overharvesting or underharvesting, will result in higher or lower than expected exploitation rates, which may increase or decrease the optimal threshold levels. If systematic management errors exist for a fishery, it is impossible to estimate optimal thresholds and exploitation rates unless the magnitude of errors is known. If known, the magnitude of the systematic errors can be used to adjust the exploitation rates. The optimal thresholds are then adjusted to the corrected exploitation rates.

In summary, factors affecting optimal thresholds can be classified at four levels of decreasing importance. The form of stock-recruitment curve (i.e., S-R γ), exploitation rate, and management objective are the three most important factors. The second group of important factors consists of environmental cycle, environmental variation, S-R α, planning horizon, density-dependent natural mortality and measurement error. Environmental autocorrelation and natural mortality patterns belong to the third group of relatively unimportant factors. In the last group, S-R β, initial biomass and implementation error are unimportant. In determining optimal threshold levels for a population with single-species dynamics, if the population approximately meets the assumptions for these factors, the first group of factors is essential, the second group should be considered, the third group may be passed by, and the last group can be completely ignored.

Chapter Seven
LIMITATIONS AND CONCLUSIONS

LIMITATIONS

The population models in this study assumed single-species dynamics. A single species approach is simple and practical, and makes data collection cost-effective. It is also routinely adopted for fisheries management and applied to modelling the dynamics of exploited fish populations (e.g., Beverton and Holt 1957; Deriso 1980; Hightower and Grossman 1985, 1987; Getz et al. 1987; Matsuda et al. 1992). Multi-species biological and technical interactions are, however, well-known to influence stock and fishery dynamics (e.g., May et al. 1979; Laevastu and Larkins 1981; Mercer 1982; Kerr and Ryder 1989). How important is the role of species interactions in determining optimal threshold levels? What implications do species interactions have on implementing threshold harvest strategies? The species interactions were briefly discussed in chapters 3, 4 and 6. The following further discusses these limitations. Another major limitation of this study is that no bioeconomic management objectives were considered in determining optimal thresholds.

Biological Interactions

Species interactions affect population dynamics directly through predation and competition, which affect growth and mortality of a population, especially during the early life from eggs to recruits. At the ecosystem level. food webs represent a static picture of the dynamic processes, predation and competition. Figure 7.1 is the partial food web for pollock and herring in the eastern Bering Sea, based on stomach content data (Perez 1990; Livingston 1991; Livingston et al. 1986, 1993). Pollock abundance is at least an order of magnitude larger than any other single fish species observed and is the central component of the food web in the eastern Bering Sea. The important prey

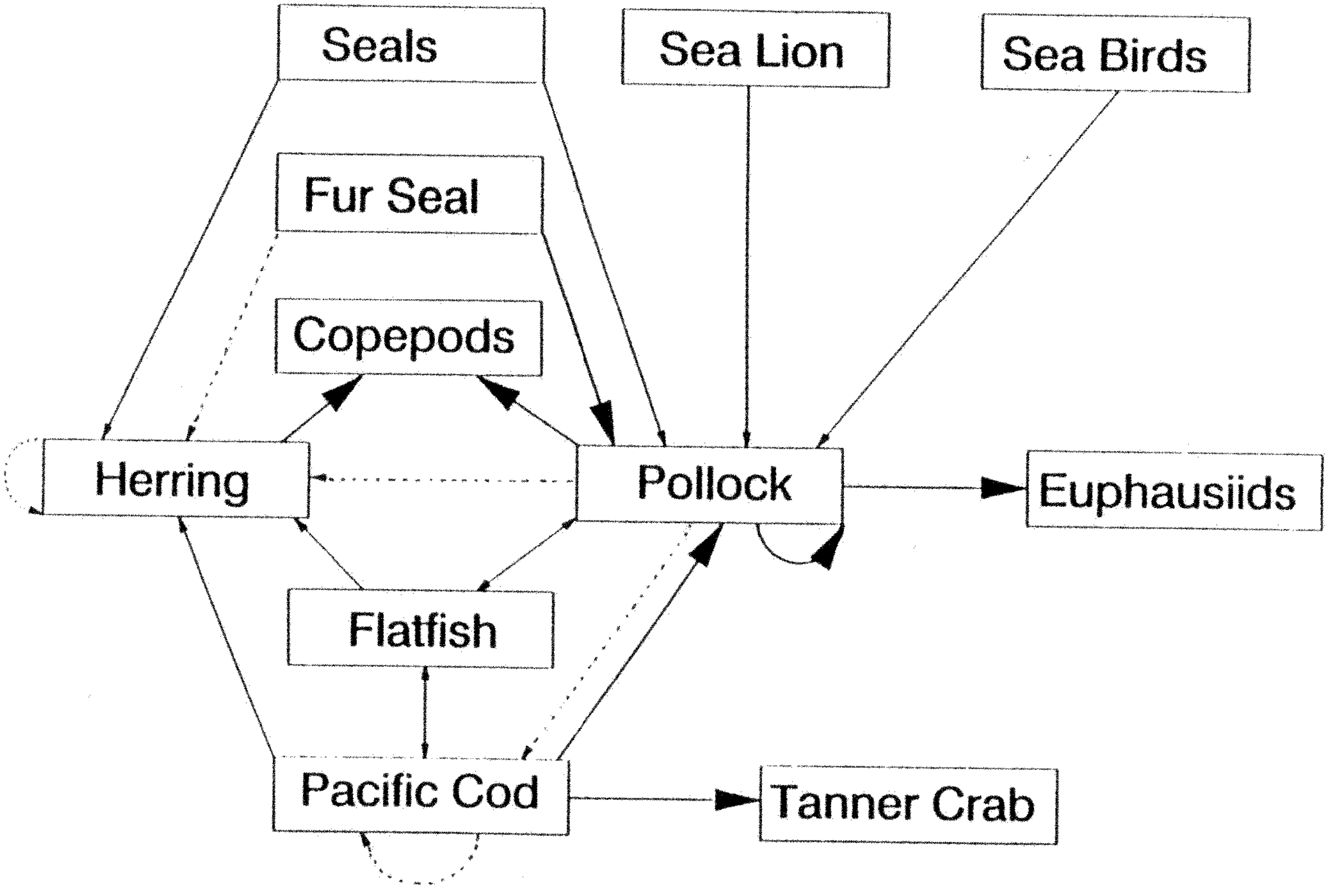

Figure 7.1. Partial food web for pollock and herring in the eastern Bering Sea, based on the stomach content data. The line types indicate the strength of the interactions: dotted line: weak; solid line: intermediate; bold line: strong. Arrows point toward prey species.

are euphausiids and copepods for juvenile pollock and juvenile pollock for adult pollock (Livingston 1991; Livingston et al. 1986, 1993). Pacific cod appears to be the most important predator of pollock (Livingston 1991; Livingston et al. 1986, 1993). The diets of sea birds and marine mammals (e.g., seals and sea lions) also include pollock, especially juvenile pollock (Perez 1990; Lowry et al. 1989; Springer and Byrd 1989).

Trophic relationships for eastern Bering Sea herring are somewhat less well understood than for pollock. Herring primarily feed on copepods, fish eggs and larvae. Flatfish, Pacific cod and seals may be important predators of herring (Livingston 1991; Livingston et al. 1993; Perez 1990). Predation on herring by groundfish in the eastern Bering Sea appears to be sporadic in time and space (Livingston 1991; Livingston et al. 1993). Although the important trophic relationships can qualitatively be identified from the stomach content data as shown in Figure 7.1, the dynamic functional relationships among them remain to be quantified because of information gaps (Smith et al. 1984; Kajimura and Fowler 1984). Species interactions for Prince William Sound herring are unclear.

Because most of predation mortality in the eastern Bering Sea occurs before recruitment, the most important effects of species interactions may be on year-class strength. A single-species approach basically assumes that mortality from eggs to recruits caused by species interactions is indistinguishable from other environmental factors. Three patterns of pre-recruitment mortality were examined in this study: randomness, autocorrelation, and periodic cycle. These three patterns may well cover the effects of species interactions on recruitment. Under management objectives as the trade-off between yield and variation in yield for a single species, the results show that randomness and autocorrelation with the observed data ranges have very minor effects on optimal threshold levels. Periodic cycles are important in determining optimal threshold levels if the amplitude of the cycle is high and the period is long. But periodic cycles of both pollock and herring recruitment are weak and affect optimal thresholds insignificantly. Furthermore, cannibalism appears to be the major source of predation mortality on pre-recruit pollock (Livingston 1989; Livingston et al. 1986, 1993) and may be accounted for by using the Ricker stock-recruitment curve. Thus, species interactions may play a minor role in pollock recruitment dynamics in the eastern Bering Sea.

In this context, it is important to distinguish between cycles in recruitment and cycles in total population biomass. Some cycles reported in the literature are biomass cycles due to the lack of long time series of recruitment data. It is easy to show that a random time series of recruitment can produce a cycling population biomass. The strongly cycling population biomass of eastern Bering Sea pollock and herring during the last three decades was caused by three to four exceptionally strong year-classes.

The effects of species interaction on adult fish may result in depensatory or compensatory natural mortality. My results show that such natural mortality has minor effects on optimal thresholds unless the mortality is extremely high. Compared to juveniles, predation mortality on adult pollock and herring in the eastern Bering Sea is relatively minor. Competition for eastern Bering Sea pollock and herring and Prince William Sound herring has not been demonstrated and is largely speculative. Overall, the effects of species interactions on optimal threshold levels of pollock and herring in the eastern Bering Sea may be minor.

If the management objectives are to protect the whole ecosystem or maximize the yield or economic returns for all commercially important species rather than a single species, species interactions may have profound effects on threshold management strategies. Although pollock recruitment may not be affected by other species, pollock recruitment may affect other species abundance, especially marine mammals and sea birds. If some marine mammals or sea birds depend mainly on pollock or herring for food, how many pollock or herring have to be saved for these marine mammals or sea birds to protect the predators? Should we reduce pollock abundance to make room for other economically more valuable species if they exist? Multi-species models and ecosystem models may help refine these questions, which in turn raise important policy issues beyond the scope of this discussion. Adaptive management may be implemented to test alternative hypotheses (Collie 1991b).

The eastern Bering Sea has been one of the most intensively studied areas in fisheries and ecosystem modelling during the last three decades. Multi-species and ecosystem models were constructed for the eastern Bering Sea more than a decade ago (Laevastu and Larkins 1981; Knechtel and Bledsoe 1981, 1983). These models have enhanced the understanding of the ecosystem, but like other ecosystem models, the precision of such models has not been high enough for management purposes. The information gaps are currently too large to make such complex models attractive for fisheries management. Although species interactions are intuitively important for population dynamics, little convincing evidence has been found that species interactions affect the abundance of predators or prey in the eastern Bering Sea. For example, there is no shortage of conflicting hypotheses about how pollock might influence sea lions in the eastern Bering Sea (Springer 1992). Not surprisingly, this problem is riddled with confusion.

Like most fisheries around the world, the fisheries in the eastern Bering Sea and other parts of Alaska have primarily been managed with a single-species approach. However, future insights about species interactions, perhaps of a radically new sort going far beyond conventional multi-species and ecosystem approaches, could offer potential alternatives to single-species approaches to fisheries management. With reliable multi-species or ecosystem models at hand, threshold management strategies at the multi-species or ecosystem levels could be evaluated and optimal thresholds estimated.

Multi-species models for simple ecosystems were examined by May et al. (1979). Mercer (1982) and Kerr and Ryder (1989) offered a variety of multi-species approaches to fisheries management. Alternative ecosystem approaches can be found in Laevastu and Larkins (1981), Knechtel and Bledsoe (1981, 1983), and Grant (1986). It appears that further work along these or different lines will be necessary before the goals of multi-species management in marine ecosystems can be achieved.

Technical Interactions

Technical interactions of multiple species offer further challenges to fisheries managers for implementing single-species threshold management strategies. Because many species share the same space in the same time, it is impossible for certain gears, especially trawl, to catch only a single species. Bycatch is the catch of non-targeted species in a fishery. Herring fisheries in Alaska occur primarily in spawning areas, and bycatch of other species is too small to be of concern. Bycatch of herring occurs in the eastern Bering Sea trawl fisheries and is very small, compared with herring abundance (Funk et al. 1990). But pollock bycatch in the eastern Bering Sea is very high because pollock is so abundant. Bycatches of other species also occur in the pollock trawl fishery.

One solution to the bycatch problem is to set bycatch limits for each fishery. Alternative solutions are to harvest targeted species when they are less mixed with other non-targeted species, to use highly selective gears to reduce bycatch rates, or to have an economic penalty for the amount of bycatch. Successful threshold management strategies may require that targeted fisheries are closed and that bycatches in non-targeted fisheries are minimized when the abundance of concerned species falls below threshold levels.

Bioeconomic Management Objectives

The objective function in this study is a linear combination of average yield and variation in yield. It will be equivalent to a trade-off between total economic value and economic stability if the price for a unit of yield is constant. The high yield may result in a low price for a unit of yield according to the conventional theory of supply and demand. Thus, maximum yield may not necessarily result in maximum economic value. Both Alaska pollock and herring products are sold in international markets, thus the prices of these fish products are affected by the catches worldwide as well. Prices may be exogenous for Alaska herring because Alaska herring products share a small proportion of the international markets. Prices are endogenous for Bering Sea pollock because it supports the largest single-species fishery in the world. On the other hand, a high price is beneficial to the fishing industry, but may hurt consumers. So total economic value for the fishing industry is not necessary equivalent to total value to the whole society if the resources belong to the whole society. Because the consumers of Alaska herring and pollock products are primarily international, it may not be a major concern for the total value to the whole society. Furthermore, maximizing profits may result in less employment opportunity for fishing communities where many fishermen regard fishing as a living style. Therefore, fisheries management objectives are complex and sometimes conflict. If total economic value is the management objective, the optimal threshold levels are affected by the relationship between the fish price and total yield. If a low yield results in a disproportionally high price, the optimal threshold levels will be very low and even close to zero.

This study did not examine the catch allocation and fishing cost, both of which are important to determine the economic profits from fishing operations. Maximizing economic profits may be a goal for an individual fisherman or a fishing company, but it is seldom a sole objective of fisheries management. Equitable allocation among different user groups may outweigh the economic profits. For example, the herring pound fishery is much more valuable than other herring fisheries per unit herring, and a fraction of the herring in the pound fishery can survive. The pound fishery in Alaska is limited to a small percent because of equitable allocation and demand for roe on kelp. Current fishing capabilities for both herring and pollock in Alaska may be far more than needed to produce MSY, but it is not easy to reduce the number of fishing vessels. For example, for some purse seine herring fisheries in Alaska, the current allowed fishing duration is 20 or 30 minutes! In such fisheries, a small fraction of the current fishing effort can easily catch the same amount of catch quota. The key to optimize economic efficiency is how to find a way to reduce the excess effort and solve overcapitalization problems which are beyond the scope of this study.

If the management objective is economic profit, there exists an economic threshold. Costs for fishing operation consist of fixed costs and variable costs (Clark 1976, 1985). Fixed costs are the capital costs of fishing companies and fishing vessels, and variable costs are the expenses occurring during fishing. If the total revenue from a fishing opening is less than the total variable cost, the population abundance is below the economic threshold and fishing shall be prohibited. The economic threshold may be smaller or greater than the biological threshold considered in this study, depending on fixed costs, variable costs, fish prices and population characteristics. If there is a strong demand for a fish product and the fish price goes up dramatically with decreasing supply, the economic threshold will be very small. If a population like herring forms schools such that catch per unit of effort is independent of population abundance, the economic threshold may be much smaller than the biological threshold. If fixed costs are high relative to variable costs, the economic threshold will be low. It is likely that the economic threshold for a population changes from year to year because the fixed and variable costs and fish prices are likely to change annually.

In bioeconomic studies, a discount rate is usually used to discount the future yield. Clark (1985) stated that "higher discount rates normally imply lower levels of resource conservation by private resource owners, other things being equal" as a fundamental principle of renewable resource economics. Because a threshold approach seeks to protect resources and enhance the future yields, discount rates are negatively associated with optimal threshold levels. A high discount rate will favor non-threshold approaches. Furthermore, a positive discount rate may result in an optimal management strategy that drives the population to extinction if the discount rate is higher than the overall population growth rate (Clark 1985). Common discount rates for public resource management range from 0 to 3% (Clark 1985). The British Columbia Salmonid Enhancement Program used a 10% discount rate for evaluating new projects (J. Collie, personal communications). In this study, a zero discount rate was used. In reality, all fisheries in Alaska have been managed with a zero discount rate and fisheries management elsewhere has rarely applied a specified positive discount rate.

CONCLUSIONS

1. The survival rates from eggs to recruits from 14 of the 19 herring stocks in the north Atlantic and northeast Pacific Oceans are significantly related to spawning

biomass, with high spawning biomass resulting in low survival rates. The year-class strengths from about 41% of the stocks are statistically associated with spawning biomass. Most stocks have compensatory, dome-shaped stock-recruitment curves.

2. Positive correlations of herring recruitment are generally found among geographically close stocks. Environmental processes may play an important role in herring recruitment dynamics within a certain spatial scale.

3. Default percentage of pristine biomass usually performs best among the threshold estimation methods. The loss of yield due to errors in threshold estimation is small, generally under 10%. About 15 to 20 years of data are required to obtain a reliable estimate of thresholds.

4. The most important factors affecting optimal threshold levels are management objectives, the form of stock-recruitment curve and fishing mortality. Environmental cycle, environmental variation, the original slope of stock-recruitment curve, planning horizon, density dependent natural mortality and measurement error also influence optimal threshold levels. Optimal thresholds are generally insensitive to environmental autocorrelation, natural mortality patterns, initial biomass and implementation error.

5. Compared to a non-threshold approach, threshold management strategies increase the long-term average yield, stabilize population abundance, shorten rebuilding time, and increase management flexibility.

6. When simultaneously optimizing threshold level and fishing mortality with the maximum yield objective, optimal fishing mortality is slightly above fishing mortality at MSY, and optimal threshold levels range from 40% to 60% of pristine biomass for eastern Bering Sea pollock, from 40% to 50% for eastern Bering Sea herring and from 30% to 60% for Prince William Sound herring. The response surfaces are flat: several combinations of fishing mortality and threshold level could produce close to the maximum yield possible.

7. With fishing mortality at MSY ($F_{MSY} = 0.42$ for EBS pollock, $H_{MSY} = 0.36$ for EBS herring, $H_{MSY} = 0.34$ for PWS herring (no-cycle recruitment), and $H_{MSY} = 0.42$ for PWS herring (cycle recruitment)) and a management objective of equal trade-off

between the increase of yield and the decrease of variation in yield, optimal thresholds range from 20% to 30% of pristine biomass, with a median of 25%, for eastern Bering Sea pollock, from 10% to 20% with a median of 20% for eastern Bering Sea herring, and from 5% to 15% with a median of 10% for Prince William Sound herring.

8. With the status quo exploitation rate of 20% and objective functions from maximum yield to equal trade-off between yield and variation in yield, optimal thresholds range from 10% to 25%, median of 20%, of pristine biomass for eastern Bering Sea herring, and from 5% to 25%, median of 15%, for Prince William Sound herring.

REFERENCES CITED

Alaska Department of Fish and Game (ADF&G). 1992. Commercial herring fishing regulations. Alaska Dept. Fish & Game, Juneau, AK.

Alaska Sea Grant College Program. 1989. Proceedings of the International Symposium on the Biology and Management of Walleye Pollock. Alaska Sea Grant Rep. 89-1: 789p.

Alton, M.S., and R.B. Deriso. 1983. Pollock, p.1-62. *In* D. H. Ito and J. W. Balsiger [ed.] Condition of Groundfish Resources of the Gulf of Alaska in 1982. NOAA Tech. Memo. NMFS F/NWC-52.

Alverson, D.L., and W.T. Pereyra. 1969. Demersal fish explorations in the northeastern Pacific Ocean---an evaluation of exploratory fishing methods and analytical approaches to stock size and yield forecasts. J. Fish. Res. Board Can. 26:1985-2001.

Anonymous. 1992. Report of the ICES advisory committee on fishery management 1991. ICES Cooperative Research Report, No. 179.

Anonymous. 1993. Report of the ICES advisory committee on fishery management 1992. ICES Cooperative Research Report, No. 193.

Anthony, V.C., and M.J. Fogarty. 1985. Environmental effects on recruitment, growth, and vulnerability of Atlantic herring (*Clupea harengus harengus*) in the Gulf of Maine region. Can. J. Fish. Aquat. Sci. 42(suppl. 1):158-173.

Archibald, C.P., D. Fournier, and B.M. Leaman. 1983. Reconstruction of stock history and development of rehabilitation strategies for Pacific Ocean perch in Queen Charlotte Sound, Canada. N. Am. J. Fish. Manage. 3:283-294.

Armstrong, M.J., and P.A. Shelton. 1988. Bias in estimation of stock-recruit function parameters caused by nonrandom environmental variability. Can. J. Fish. Aquat. Sci. 45:554-557.

Bailey, K., R. Francis, and J. Schumacher. 1986. Recent information on the causes of variability in recruitment of Alaska pollock in the eastern Bering Sea: Physical conditions and biological interactions. Int. N. Pac. Fish. Comm. Bull. 47:155-165.

Baker, T.T. 1991. Cohort analysis of Pacific herring in the Togiak district, Alaska, 1980-1990, p.403-426. *In* Proc. Int. Herring Symp., Alaska Sea Grant Rep. 91-01.

Bakkala, R.G. [ed.] 1988. Condition of groundfish resources of the eastern Bering Sea and Aleutian Islands region in 1987. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-139: 219p.

Bakkala, R.G., V.G. Wespestad, and L.-L. Low. 1987. Historical trends in abundance and current condition of walleye pollock in the eastern Bering Sea. Fish. Res. 5:199-215.

Becker, R.A., J.M. Chambers, and A.R. Wilks. 1988. The new S language: a programming environmental for data analysis and graphics. Wadsworth & Brooks/Cole, Pacific Grove, CA. 702p.

Beddington, J.R., and J.G. Cooke. 1983. The potential yield of fish stocks. FAO Fish. Tech. Pap., (242): 47p.

Beverton, R.J.H., and S.J. Holt. 1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric. Fish. Food G. B. (2 Sea Fish.), 919): 533p.

Bucher, W.A., and L. Hammarstrom. 1993. 1992 Lower Cook Inlet area annual finfish management report. Alaska Dept. of Fish and Game, Div. Commer. Fish., Regional Information Report No. 2A93-11. Anchorage, AK. 133p.

Buck, R.J.G., and D.W. Hay. 1984. The relation between stock size and progeny of Atlantic salmon, *Salmo salar* L., in a Scottish stream. J. Fish. Biol. 23:1-11.

Burkey, C. 1986. Population structure of Pacific herring (*Clupea harengus pallasi*) in eastern Prince William Sound, Alaska. Master's Thesis, University of Alaska, Juneau, AK.

Chang, S. 1974. An evaluation of the eastern Bering Sea fishery for Alaska pollock (*Theragra chalcogramma*): population dynamics. Ph. D. Dissertation, University of Washington, Seattle, WA., 281p.

Chebanov, N.A. 1989. Forecasts of runs of west Kamchatka pink salmon (*Oncorhynchus gorbuscha*) based on analysis of the downstream migration and inshore feeding of juveniles, p.161-168. *In* R. J. Beamish and G. A. McFarlane [ed.] Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models. Can. Spec. Publ. Fish. Aquat. Sci. 108.

Clark, C.W. 1976. Mathematical Bioeconomics: The Optimal Management of Renewable Resources. Wiley-Interscience, New York, NY. 357p.

Clark, C.W. 1985. Bioeconomic Modelling and Fisheries Management. Wiley-Interscience, New York, NY. 291p.

Clark, W.G. 1991. Groundfish exploitation rates based on life history parameters. Can. J. Fish. Aquat. Sci. 48:734-750.

Collie, J.S. 1991a. Herring population dynamics and management in Sitka Sound, Alaska, p.463-476. *In* Proc. Int. Herring Symp., Alaska Sea Grant Rep. 91-01.

Collie, J.S. 1991b. Adaptive strategies for management of fisheries resources in large marine ecosystems, p.225-242. *In* K. Sherman, L.M. Alexander, and B.D. Gold [ed.] Food chains, yields, models, and management of large marine ecosystems. Westview Press. San Francisco, CA.

Collie, J.S., and P.D. Spencer. *in press*. Management strategies for fish populations subject to low-frequency environmental forcing. *In* Proc. Int. Symp. Harvest Strat. for Expl. Fish Pop. Alaska Sea Grant Rep. 93-02.

Conover, W.J. 1980. Practical Nonparametric Statistics. Second Edition. John Wiley & Sons, New York, NY. 493p.

Corten, A. 1986. On the causes of the recruitment failure of herring in the central and northern North Sea in the years 1972-1978. J. Cons. int. Explor. Mer, 42:281-294.

Csirke, J. 1980. Recruitment in the Peruvian anchovy and its dependence on the adult population. Rapp. P.-v. Reun. cons. int. Explor. Mer, 177:307-313.

Cushing, D.H. 1971. The dependence of recruitment on parent stock in different groups of fishes. J. Cons. int. Explor. Mer, 33:340-362.

Cushing, D.H. 1973. Dependence of recruitment on parent stock. J. Fish. Res. Board Can. 30:1965-1976.

Cushing, D.H. 1977. The problems of stock and recruitment, p.116-133. *In* J.A. Gulland [ed.] Fish Population Dynamics. 1st Edition. John Wiley & Sons, New York, NY.

Cushing, D.H. 1982. Climate and Fisheries. Academic Press, London. 373p.

Cushing, D.H., and J.G.K. Harris. 1973. Stock and recruitment and the problem of density-dependence. Rapp. P.-v. Reun. Cons. Explor. Perm. Int. Mer, 164:142-155.

Davydov, I.V. 1989. Characteristics of development of atmospheric circulation in the northern Pacific Ocean and their role in determining long-term changes in the abundance of certain fishes, p.181-194. *In* R. J. Beamish and G. A. McFarlane [ed.] Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models. Can. Spec. Publ. Fish. Aquat. Sci. 108.

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

Deriso, R.B. 1985. Risk adverse harvesting strategies. p.65-74. *In* M. Mangel [ed.] Proceedings of the Second Ralf Yorque Workshop, Lecture notes in biomathematics (61). Springer- Verlag, New York, NY.

Deriso, R.B. 1987. Optimal $F_{0.1}$ criteria and their relationship to maximum sustainable yield. Can. J. Fish. Aquat. Sci. 44(Suppl. 2):339-348.

Deriso, R.B., T.J. Quinn II, and P.R. Neal. 1985. Catch-age analysis with auxiliary information. Can. J. Fish. Aquat. Sci. 42:815-824.

Deriso, R.B., P.R. Neal, and T.J. Quinn II. 1989. Further aspects of catch-age-analysis with auxiliary information, p.137-150. *In* R. J. Beamish and G. A. McFarlane [ed.] Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models. Can. Spec. Publ. Fish. Aquat. Sci. 108.

Donnelly, R.F. 1983. Factors affecting the abundance of Kodiak Archipelago pink salmon (*Oncorhynchus gorbuscha*, Walbaum). Ph. D. dissertation, University of Washington, Seattle, WA., 157p.

Dragesund, O., J. Hamre, and O. Ulltang. 1980. Biology and population dynamics of the Norwegian spring-spawning herring. Rapp. P.-v. Reun. Cons. int. Explor. Mer, 177:43-71.

Fargo, J., and A.V. Tyler [ed.] 1989. Groundfish stock assessments for the west coast of Canada in 1988 and recommended yield options for 1989. Can. Tech. Rep. Fish. Aquat. Sci. 1646: 294p.

Fowler, C.W. 1981. Density dependence as related to life history strategy. Ecology 62:602-610.

Fowler, C.W. 1988. Population dynamics as related to rate of increase per generation. Evol. Ecol. 2:197-204.

Fried, S. M., and V. G. Wespestad. 1985. Productivity of Pacific herring (*Clupea harengus pallasi*) in the eastern Bering Sea under various patterns of exploitation. Can. J. Fish. Aquat. Sci. 42(Supp. 1):181-191.

Funk, F.C. 1991. Harvest policy implications of yield per recruit models for Pacific herring in Alaska, p.453-462. *In* Proc. Int. Herring Symp., Alaska Sea Grant Rep. 91-01.

Funk, F.C., and M. Harris. 1992. Preliminary forecasts of catch and stock abundance for 1992 Alaska herring fisheries. Alaska Dept. of Fish and Game, Div. Commer. Fish., Regional Information Report No. 5J92-04, Juneau, 114p.

Funk, F.C., and G.J. Sandone. 1990. Catch-age analysis of Prince William Sound, Alaska, herring, 1973-1988. Alaska Dept. of Fish and Game, Div. Commer. Fish., Fishery Research Bulletin 90-01, 36p.

Funk, F., L. Waston, and R. Berning. 1990. Revised estimates of the bycatch of herring in 1989 Bering Sea trawl fisheries. Alaska Dept. of Fish and Game, Div. Commer. Fish., Regional Information Report No. 5J90-01, Juneau, 45p.

Funk, F. C., and J. Zheng. 1992a. Age-structured analysis of Prince William Sound herring. Alaska Dept. of Fish and Game, Div. Commer. Fish., Regional Information Report No. 5J92-00, Juneau.

Funk, F. C., and J. Zheng. 1992b. Precision of implementing harvest objectives in Alaska herring fisheries. Manuscript.

Garrod, D.J. and B.W. Jones. 1974. Stock and recruitment relationship in the northeast Arctic cod stock and the implications for management of the stock. J. Cons. int. Explor. Mer, 36(1):35-41.

Gatto, M., and S. Rinaldi. 1976. Mean value and variability of fish catches in fluctuating environments. J. Fish. Res. Board Can. 33:189-193.

Getz, W.M., R.C. Francis, and G.L. Swartzman. 1987. On managing variable marine fisheries. Can J. Fish. Aquat. Sci. 44:1370-1375.

Getz, W.M., and R.G. Haight. 1989. Population Harvesting: Demographic Models of Fish, Forest, and Animal Resources. Princeton Univ. Press, Princeton, NJ. 391p.

Getz, W.M., and G.L. Swartzman. 1981. A probability transition matrix model for yield estimation in fisheries with highly variable recruitment. Can. J. Fish. Aquat. Sci. 38:847-855.

Grant, W.E. 1986. System analysis and simulation in wildlife and fisheries sciences. John Wiley & Sons, New York, NY. 338p.

Grant, W.S., and F.M. Utter. 1984. Biochemical population genetics of Pacific herring (*Clupea pallasi*). Can. J. Fish. Aquat. Sci. 41:856-864.

Grosse, D. J, and J. E. Purcell. 1990. Cannibalism in Pacific herring: not so trivial after all?, p.13-14. *In* M.F. O'Toole [ed.] Proc. of the Sixth Pacific Coast Herring Workshop. Wash. Dept. Fish. Prog. Rep. No. 279: 105p.

Gulland, J.A. 1983. Fish Stock Assessment: a Manual of Basic Methods. John Wiley and Sons, Chichester, UK. 223p.

Gulland, J.A., and L.K. Boerema. 1973. Scientific advice on catch levels. Fish. Bull. 71:325-335.

Haegele, C.W., and J.F. Schweigert. 1985. Distribution and characteristics of herring spawning grounds and description of spawning behavior. Can. J. Fish. Aquat. Sci. 42 (Suppl. 1): 39-55.

Haist, V. 1990. An evaluation of three harvest strategies based on forecast stock biomass for B. C. herring fisheries, p.90-99. *In* M. F. O'Toole [ed.]. Proc. of the Sixth Pacific Coast Herring Workshop. Wash. Dept. Fish. Prog. Rep. No. 279: 105p.

Haist, V., D.A. Fournier, and J.F. Schweigert. *in press*. Estimation of density-dependent natural mortality in British Columbia herring stocks through SSPA and its impact on sustainable harvesting strategies, p.000-000. *In* S.J. Smith [ed.] Risk evaluation and biological reference points for fisheries management. Can. Spec. Publ. Fish. Aquat. Sci. 000.

Haist, V., and J.F. Schweigert. 1990. Stock assessments for British Columbia herring in 1989 and forecasts of the potential catch in 1990. Can. MS Rep. Fish. Aquat. Sci. 2049: 62p.

Hall, D.L., R. Hilborn, M. Stocker, and C.J. Walters. 1988. Alternative harvest strategies for Pacific herring (*Clupea harengus pallasi*). Can. J. Fish. Aquat. Sci. 45: 888-897.

Hamner, H.H., and C. Kerkvliet. 1992. Pacific herring stocks and fisheries in the Arctic-Yukon-Kuskokwim region of the Bering Sea, Alaska, 1992, a report to the Alaska Board of Fisheries. Alaska Dept. of Fish and Game, Div. Commer. Fish., Regional Information Report No. 3A92-27. 133p. Anchorage, AK. 30p.

Hennemuth, R.C., J.E. Palmer, and B.E. Brown. 1980. A statistical description of recruitment in eighteen selected fish stocks. J. Northw. Atl. Fish. Sci. Vol. 1:101-111.

Hightower, J.E., and G.D. Grossman. 1985. Comparison of constant effort harvest policies for fish stocks with variable recruitment. Can. J. Fish. Aquat. Sci. 42:982-988.

Hightower, J.E., and G.D. Grossman. 1987. Optimal policies for rehabilitation of overexploited fish stocks using a deterministic model. Can. J. Fish. Aquat. Sci. 44:803-810.

Hightower, J.E., and W.H. Lenarz. 1989. Optimal harvesting policies for the widow rockfish fishery, p.83-91. *In* E. F. Edwards and B. A. Megrey [ed.] Mathematical analysis of fish stock dynamics. Am. Fish. Soc. Symp. 6.

Hilborn, R. 1979. Comparison of fisheries control systems that utilize catch and effort data. J. Fish. Res. Board Can. 36:1477-1489.

Hilborn, R. 1985. A comparison of harvest policies for mixed stock fisheries, p.74-87. *In* M. Mangel [ed.] Proc. of the Second Ralf Yorque Workshop, Lecture Notes in Biomathematics (61). Springer-Verlag, New York, NY.

Ho, Y.-C. 1970. Differential games, dynamic optimization, and generalized control theory. J. Optim. Theory and Appl. 6:179-209.

Hollowed, A.B. 1990. Recruitment of marine fishes in the northeast Pacific ocean in relation to interannual variations in the environment. Ph. D. dissertation, University of Washington, Seattle, WA., 281p.

Hollowed, A.B., K.M. Bailey, and W.S. Wooster. 1987. Patterns of recruitment of marine fishes in the northeast Pacific ocean. Biol. Oceano. 5:99-131.

Hollowed, A.B., and B.A. Megrey. *in press*. Evaluation of risks associated with application of alternative harvest strategies for Gulf of Alaska walleye pollock. *In* Proc. Int. Symp. Harvest Strat. for Expl. Fish Pop. Alaska Sea Grant Rep. 93-02.

Honkalehto, T. 1989. A length-cohort analysis for walleye pollock based on empirical estimation of cannibalism and predation by marine mammals, p.651-666. *In* Proc. Int. Symp. Biol. Manage. Walleye Pollock. Alaska Sea Grant Rep. 89-1.

Horwood, J.W. 1987. A calculation of optimal fishing mortalities. J. Cons. int. Explor. Mer, 43:199-208.

Hourston, A.S. 1980. The decline and recovery of Canada's Pacific herring stocks. Rapp. P.-v. Reun. Cons. int. Explor. Mer, 177:143-153.

Huang, B., and C.J. Walters. 1983. Cohort analysis and population dynamics of large yellow croaker in the China Sea. N. Amer. J. Fish. Manag. 3:295-305.

International Council for Exploration of the Sea (ICES). 1984. Report of the working group on methods of fish stock assessment. ICES C. M. 1984/Assess 19.

Jakobsson, J. 1980. Exploitation of the Icelandic spring- and summer-spawning herring in relation to fisheries management, 1947-1977. Rapp. P.-v. Reun. Cons. int. Explor. Mer, 177:23-42.

Jakobsson, J. 1985. Monitoring and management of the northeast Atlantic herring stocks. Can. J. Fish. Aquat. Sci. 42(Suppl. 1):207-221.

Kajimura, H. 1984. Opportunistic feeding of the northern fur seal, *Callorhinus ursinus*, in the eastern North Pacific Ocean and eastern Bering Sea. U. S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-779., 49p.

Kajimura, H., and C. W. Fowler. 1984. Apex predators in the walleye pollock ecosystem in the eastern Bering Sea and Aleutian Islands Regions, p.193-134. *In* D.H. Ito [ed.] Proc. of the workshop on walleye pollock and its ecosystem in the eastern Bering Sea. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-62.

Kerr, S.R., and R.A. Ryder. 1989. Current approaches to multispecies analyses of marine fisheries. Can. J. Fish. Aquat. Sci. 46:528-534.

Knechtel, C.D., and L.J. Bledsoe. 1981. A numerical simulation model of the population dynamics of walleye pollock, *Theragra chalcogramma* (Pallas 1811), in a simplified ecosystem: Part I, Model description. U.S. Dep. Commer., NOAA Tech. Memo., NMFS F/NWC-50. 264p.

Knechtel, C.D., and L.J. Bledsoe. 1983. A numerical simulation model of the population dynamics of walleye pollock, *Theragra chalcogramma* (Pallas 1811), in a simplified ecosystem: Part II, Model calibration, validation, and exercise. U.S. Dep. Commer., NOAA Tech. Memo., NMFS F/NWC-50. 264p.

Koslow, J.A. 1984. Recruitment patterns in northwest Atlantic fish stocks. Can. J. Fish. Aquat. Sci. 41:1722-1729.

Koslow, J.A. 1989. Managing nonrandomly varying fisheries. Can. J. Fish. Aquat. Sci. 46:1302-1308.

Koslow, J.A. 1992. Fecundity and the stock-recruitment relationship. Can. J. Fish. Aquat. Sci. 49:210-217.

Koslow, J.A., K.R. Thompson, and W. Silvert. 1987. Recruitment to northwest Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) stocks: influence of stock size and climate. Can. J. Fish. Aquat. Sci. 44:26-39.

Laevastu, T., and F. Favorite. 1976. Dynamics of pollock and herring biomasses in the eastern Bering Sea (An introductory study of fluctuations of pollock and herring stocks using preliminary 8-component Dynamic Numerical Marine Ecosystem Model). Processed Rep., 50p. Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115.

Laevastu, T., and H.A. Larkins. 1981. Marine Fisheries Ecosystem, its Quantitative Evaluation and Management. Fishing News Books Ltd., Farnham, Surrey, England. 159p.

Lande, R. 1987. Extinction thresholds in demographic models of territorial populations. Am. Naturalist 130:624-635.

Lasker, R. 1978. The relation between oceanographic conditions and larval anchovy food in the California current: identification of factors contributing to recruitment failure. Rapp. P.-v. Reun. Cons. int. Explor. Mer, 173:212-230.

Livingston, P.A. 1989. Interannual trends in walleye pollock cannibalism in the eastern Bering Sea, p.275-296. *In* Proc. Int. Symp. Biol. Manage. Walleye Pollock, Alaska Sea Grant Rep. 89-1.

Livingston, P.A. 1991. Groundfish food habits and predation on commercially important prey species in the eastern Bering Sea from 1984 to 1986. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-207. 239p.

Livingston, P.A., D.A. Dwyer, D.L. Wencker, M.S. Yang, and G.M. Lang. 1986. Trophic interactions of key fish species. Int. N. Pac. Fish. Comm., Bull. 47:49-

65.

Livingston, P.A., A. Ward, G.M. Lang, and M-S. Yang. 1993. Groundfish food habits and predation on commercial important prey species in the eastern Bering Sea from 1987 to 1989. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-11, 192p.

Low, L.L. 1974. A study of four major groundfish fisheries of the Bering Sea. Ph. D. Dissertation, University of Washington, Seattle, WA., 240p.

Lowry, L.F., K.J. Frost, and T.R. Loughlin. 1989. Importance of walleye pollock in the diets of marine mammals in the Gulf of Alaska and Bering Sea, and implications for fishery management, p.701-726. *In* Proc. Int. Symp. Biol. Mgmt. Walleye Pollock, Alaska Sea Grant Rep. 89-1.

MacArthur, R.H. 1972. Geographical Ecology. Harper and Row, New York, NY. 269p.

Matsuda, H., T. Kishida, and T. Kidachi. 1992. Optimal harvesting policy for chub mackerel (*Scomber japonicus*) in Japan under a fluctuating environment. Can. J. Fish. Aquat. Sci. 49:1796-1800.

May, R.M. 1980. Mathematical models in whaling and fisheries management. Lectures on Mathematics in the Life Sciences 13:1-64.

May, R.M., J.R. Beddington, C.W. Clark, S.J. Holt, and R.M. Laws. 1979. Management of multispecies fisheries. Science 205, No. 4403:267-277.

Mercer, M.C. 1982. Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59.

Mito, K. 1990. Estimation of consumption number by cannibalism of pollock in the eastern Bering Sea under assumption of multi-stocks. Int. N. Pac. Fish. Comm., Bull. 50:179-205.

Mode, C.J., and M.E. Jacobson. 1987a. A study of the impact of environmental stochasticity on extinction probabilities by Monte Carlo integration. Math. Biosci. 83:105-125.

Mode, C.J., and M.E. Jacobson. 1987b. On estimating critical population size for an endangered species in the presence of environmental stochasticity. Math. Biosci. 85:185-209.

Morita, S. 1985. History of the herring fishery and review of artificial propagation techniques for herring in Japan. Can. J. Fish. Aquat. Sci. 42(Suppl. 1):222-229.

Murphy, G.I. 1968. Pattern in life history and the environment. Am. Naturalist 102:391-403.

New England Fishery Management Council (NEFMC). 1985. Fishery management plan, environmental impact statement, regulatory impact review, and initial regulatory flexibility analysis for the northeast multispecies fishery. N. Engl. Fish. Manage. Counc., Saugus, MA.

North Pacific Fishery Management Council (NPFMC). 1990. Environmental assessment for Amendment 1 to the fishery management plan for the commercial king and Tanner crab fisheries in the Bering Sea/Aleutian Islands. 27p.

North Pacific Fishery Management Council (NPFMC). 1991. Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands region as projected for 1992. Complied by the Plan Team for the Groundfish Fisheries of the Bering Sea and Aleutian Islands. 401p.

Northeast Fisheries Center (NEFC). 1992. Report of the thirteenth northeast regional stock assessment workshop. NMFS Northeast Fisheries Center, Woods Hole.

Overholtz, W.J., M.P. Sissenwine and S.H. Clark. 1986. Recruitment variability and its implication for managing and rebuilding the Georges Bank haddock. Can. J. Fish. Aquat. Sci. 43:748-753.

Parma, A.M. 1990. Optimal harvesting of fish populations with non-stationary stock-recruitment relationships. Nat. Res. Mod. 4:39-76.

Penn, J.W., and N. Caputi. 1986. Spawning stock-recruitment relationships and environmental influences on the tiger prawn (*Penaeus esculentus*) fishery in Exmouth Gulf, Western Australia. Aus. J. Mar. Freshw. Res., 37:491-505.

Pepin, P. 1990. Biological correlates of recruitment variability in North Sea fish stocks. J. Cons. int. Explor. Mer, 47:89-98.

Perez, M.A. 1990. Review of marine mammal population and prey information for Bering Sea ecosystem studies. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-186, 81p.

Peterman, R.M. 1981. Form of random variation in salmon smolt-to-adult relations and its influence on production estimates. Can. J. Fish. Aquat. Sci. 38:1113-1119.

Quinn, T.J., II. 1986. Are age-structured data and analysis necessary for fisheries management? Proc. of the XIIIth International Biometrics Conference, Biometrics Soc., Seattle, WA. 12p.

Quinn, T.J., II, and J.S. Collie. 1990. Alternative estimators of walleye pollock in the eastern Bering Sea. Int. N. Pac. Fish. Comm., Bull. 50:243-258.

Quinn, T.J., II, and R.B. Deriso, S.H. Hoag, and R.J. Myhre. 1984. A summary of methods of estimating annual surplus production for the Pacific halibut fishery. Int. North Pac. Fish. Comm., Bull. 42:73-81.

Quinn, T.J., II, R. Fagen and J. Zheng. 1990. Threshold management policies for exploited populations. Can. J. Fish. Aquat. Sci. 47:2016-2029.

Quinn, T.J., II, and H.J. Niebauer. *in press*. Relation of eastern Bering Sea walleye pollock (*Theragra chalcogramma*) recruitment to environmental and oceanographic variables. *In* Proc. Int. Symp. on Climate Change and N. Fish Pop. Can. Sp. Pub. Fish. Aquat. Sci.

Reed, W.J. 1979. Optimal escapement levels in stochastic and deterministic harvesting models. J. Environ. Econ. Manage. 6:350-363.

Reed. W.J. 1980. Optimum age-specific harvesting in a nonlinear population model. Biometrics 36:579-593.

Ricker, W.R. 1954. Stock and recruitment. J. Fish. Res. Board Can. 11:559-623.

Ricker, W.R. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: 382p.

Rorres, C., and W. Fair. 1975. Optimal harvesting policy for an age-specific population. Mathe. Biosci. 24:31-47.

Rothschild, B.J. 1986. Dynamics of Marine Fish Populations. Harvard University Press, Cambridge, MA. 277p.

Rothschild, B.J., and A.J. Mullen. 1985. The information content of stock-and-recruitment data and its non-parametric classification. J. Cons. int. Explor. Mer, 42:116-124.

Ruppert, D., R.L. Reish, R.B. Deriso, and R.J. Carroll. 1984. Optimization using stochastic approximation and Monte Carlo simulation (with application to harvesting of Atlantic menhaden). Biometrics 40:535-545.

Ruppert, D., R.L. Reish, R.B. Deriso and R.J. Carroll. 1985. A stochastic population model for managing the Atlantic menhaden (*Brevoortia tyrannus*) fishery and assessing managerial risks. Can. J. Fish. Aquat. Sci. 42:1371-1379.

Sandone, G.J., S. Sharr, and J.A. Brady. 1988. Prince William Sound commercial harvest of Pacific herring, 1984-1987. Alaska Dept. of Fish and Game, Div. Commer. Fish., Fishery Research Bulletin 88-08. 61p.

SAS Institute Inc. 1988. SAS/ETS user's guide, version 6. first edition, Gary, NC: SAS Institute Inc. 560p.

Schmidt, D., and D. Pengilly. 1990. Management plan for westward region king crab stocks: Kodiak Island red king crab, Bristol Bay red king crab, St. Matthew blue king crab, Pribilof Islands blue king crab. Alaska Dept. of Fish and Game, Div. Commer. Fish., Regional Information Report 4K90-36, Kodiak, 66p.

Schweigert, J.F., C.W. Haegele, and M. Stocker. 1985. Optimizing sampling design for herring spawn surveys in the Strait of Georgia. B.C. Can. J. Fish. Aquat. Sci. 42:1806-1814.

Schweigert, J.F., V. Haist, and C. Fort. 1993. Stock assessment for British Columbia herring in 1992 and forecasts of the potential catch in 1993. Can. Tech. Rep. Fish. Aquat. Sci. 1913: 111p.

Schweigert, J.F., and D.J. Noakes. 1991. Forecasting Pacific herring (*Clupea harengus pallasi*) recruitment from spawner abundance and environmental information. p.373-387. *In* Proc. Int. Herring Symp., Alaska Sea Grant Rep. 91-01.

Schaefer, M.B. 1957. Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. Bull. inter-Amer. Trop. Tuna Comm. 1:27-56.

Shaffer, M.L. 1981. Minimum population sizes for species conservation. BioScience 31:131-134.

Shaffer, M.L. 1983. Determining minimum viable population sizes for the grizzly bear. Int. Conf. Bear Res. Manage. 5:133-139.

Shaffer, M.L. 1987. Minimum viable populations: coping with uncertainty, p.69-85. *In* M. E. Soule [ed.] Viable Populations for Conservation. Cambridge University Press. Cambridge, MA, and New York, NY.

Shepherd, J.G. 1982. A versatile new stock-recruitment relationship for fisheries, and the construction of sustainable yield curves. J. Cons. int. Explor. Mer, 40(1): 67-75.

Shepherd, J.G., J.G. Pope, and R.D. Cousens. 1984. Variations in fish stocks and hypotheses concerning their links with climate. Rapp. P.-v. Reun. Cons. int. Explor. Mer, 185:255-267.

Sigler, M.F., and J.T. Fujioka. *in press*. A comparison of policies for harvesting sablefish, *Anoplopoma fimbria*, in the Gulf of Alaska. *In* Proc. Int. Symp. Harvest Strat. for Expl. Fish Pop. Alaska Sea Grant Rep. 93-02.

Sissenwine, M.P., and J.G. Shepherd. 1987. An alternative perspective on recruitment overfishing and biological reference points. Can. J. Fish. Aquat. Sci. 44:913-918.

Smith, G.B. 1981. The biology of walleye pollock, p.527-551. *In* D. W. Hood and J. A. Calder [ed.] The eastern Bering Sea shelf: oceanography and resources, Vol. 1. U.S. Dep. Commer., NOAA., Officer Mar. Poll. Assess., Washington, D.C., USA.

Smith, G.B., M.J. Allen, and G.E. Walters. 1984. Relationships between walleye pollock, other fish, and squid in the eastern Bering Sea, p.161-192. *In* D.H. Ito [ed.] Proceedings of the workshop on walleye pollock and its ecosystem in the eastern Bering Sea. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-62.

Soule, M.E. [ed.] 1987. Viable Populations for Conservation. Cambridge University Press, Cambridge, MA, and New York, NY. 189p.

Springer, A.M. 1992. A review: walleye pollock in the North Pacific---how much difference do they really make? Fish. Oceano. 1, issue 1:80-96.

Springer, A.M., and G.V. Byrd. 1989. Seabird dependence on walleye pollock in the southeastern Bering Sea, p.667-677. *In* Proc. Int. Symp. Biol. Mgmt. Walleye Pollock, Alaska Sea Grant Rep. 89-1.

Stocker, M., V. Haist, and D. Fournier. 1985. Environmental variation and recruitment of Pacific herring (*Clupea harengus pallasi*) in the Strait of Georgia. Can. J. Fish. Aquat. Sci. 42(Suppl. 1):174-180.

Stocker, M., and D.J. Noakes. 1988. Evaluating forecasting procedures for predicting Pacific herring (*Clupea harengus pallasi*) recruitment in British Columbia. Can.

J. Fish. Aquat. Sci. 45:928-935.

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.

Tang, Q., J. Deng, and J. Zhu. 1989. A family of Ricker SRR curves of the prawn (*Penaeus orientalis*) under different environmental conditions and its enhancement potential in the Bohai Sea, p.335-339. *In* R. J. Beamish and G. A. McFarlane [ed.] Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models. Can. Spec. Publ. Fish. Aquat. Sci. 108.

Taylor, F.H.C. 1971. Variation in hatching success in Pacific herring (*Clupea pallasi*) eggs with water depth, temperature, salinity and egg mass thickness. Rapp. P.-v. Reun. Cons. Int. Explor. Mer, 160:34-41.

Thompson, G.G. *in press.* A proposal for a threshold stock size and maximum fishing mortality rate, p.000-000. *In* S.J. Smith [ed.] Risk evaluation and biological reference points for fisheries management. Can. Spec. Publ. Fish. Aquat. Sci. 000.

Thompson, K.R., and F.H. Page. 1989. Detecting synchrony of recruitment using short, autocorrelated time series. Can. J. Fish. Aquat. Sci. 46:1831-1838.

Trumble, R.J., and R.D. Humphreys. 1985. Management of Pacific herring (*Clupea harengus pallasi*) in the eastern Pacific Ocean. Can. J. Fish. Aquat. Sci. 42 (Suppl. 1):230-244.

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

Walters, C.J. 1986. Adaptive Management of Renewable Resources. Macmillan Publ. Co., New York, NY. 374p.

Walters, C.J., and J. S. Collie. 1988. Is research on environmental factors useful to fisheries management? Can. J. Fish. Aquat. Sci. 45:1845-1854.

Walters, C.J., and R. Hilborn. 1976. Adaptive control of fishing systems. J. Fish. Res. Board Can. 33:145-159.

Walters, C.J., and D. Ludwig. 1981. Effects of measurement errors on the assessment of stock-recruitment relationships. Can. J. Fish. Aquat. Sci. 38:704-710.

Walters, C.J., M. Stocker, A.V. Tyler, and S.J. Westrheim. 1986. Interaction between Pacific cod (*Gadus macrocephalus*) and herring (*Clupea harengus pallasi*) in the Hecate Strait, British Columbia. Can. J. Fish. Aquat. Sci. 43:830-837.

Ware, D.M. 1985. Life history characteristics, reproductive value, and resilience of Pacific herring (*Clupea harengus pallasi*). Can. J. Fish. Aquat. Sci. 42 (Suppl. 1):127-137.

Ware, D.M., and G.A. McFarlane. 1986. Relative impact of Pacific hake, sablefish and Pacific cod on west coast of Vancouver Island herring stocks. Int. N. Pac. Fish. Comm., Bull. 47:67-77.

Ware, D.M., and G.A. McFarlane. 1989. Fisheries production domains in the northeast Pacific Ocean, p. 359-379. *In* R. J. Beamish and G. A. McFarlane [ed.] Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models. Can. Spec. Publ. Fish. Aquat. Sci. 108.

Wespestad, V.G. 1991. Pacific herring population dynamics, early life history, and recruitment variation relative to eastern Bering Sea oceanographic factors. Ph. D. Dissertation, University of Washington, Seattle. WA., 237p.

Wespestad, V.G., and J.M. Terry. 1984. Biological and economic yields for eastern Bering Sea walleye pollock under differing fishing regimes. N. Am. J. Fish. Manage. 4:204-215.

Wespestad, V.G., and J.J. Traynor. 1988. Walleye pollock, p.11-32. *In* R.G. Bakkala [ed.] Condition of Groundfish Resources of the Eastern Bering Sea and Aleutian Islands Region in 1987. U.S. Dep. Commer.. NOAA Tech. Memo. NMFS F/NWC-139.

Wheeler, J.P., R. Chaulk, and G.H. Winters. 1985. East coast Newfoundland herring - 1984 assessment. CAFSAC Res. Doc. 85/90. 75p.

Winters, G.H., and J.P. Wheeler. 1987. Recruitment dynamics of spring-spawning herring in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. 44:882-900.

Wissel, C., and S. Stocker. 1991. Estimation of populations by random influences. Theor. Pop. Biol. 39:315-328.

Zebdi, A., and J.S. Collie. *in press*. Effect of climate on herring population dynamics in the northeast Pacific Ocean. *In* Proc. Int. Symp. on Climate Change and N. Fish Pop. Can. Sp. Pub. Fish. Aquat. Sci.

Zheng, J., F.C. Funk, G.H. Kruse, and R. Fagen. *in press* a. Evaluation of threshold management strategies for Pacific herring in Alaska. *In* Proc. Int. Symp. Harvest Strat. for Expl. Fish Pop. Alaska Sea Grant Rep. 93-02.

Zheng, J., T.J. Quinn II, and G.H. Kruse. *in press* b. Comparison and evaluation of threshold estimation methods for exploited fish populations. *In* Proc. Int. Symp. Harvest Strat. for Expl. Fish Pop. Alaska Sea Grant Rep. 93-02.