

**DECISION DYNAMICS AT SEA: AN APPLICATION OF  
FORAGING THEORY TO THE STUDY OF FISHING EFFORT**

by

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B.Sc., Dalhousie University, 1982

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**DECISION DYNAMICS AT SEA: AN APPLICATION OF FORAGING  
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Decision dynamics at sea: an application of foraging theory to the study  
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## Abstract

Fishermen make decisions at sea that potentially bias the statistics derived from catch and effort data. Movement of vessels to maximize catch rates leads to catches that are a non-random sample of fish populations. Furthermore, the unreported discarding and mortality of less valuable fish (high-grading) biases stock assessments that are based on the amount of landed fish. Foraging theory provides a theoretical basis for the prediction of fishermen's decisions at sea. I used foraging theory to develop and test hypotheses about the behavior of fishermen and to examine the implications of their behavior for fisheries management.

The ideal free distribution (IFD) predicts that interference competition among foragers affects their spatial distribution and results in equal benefits to all individuals. When fishing vessels follow an IFD among several populations of fish, local catch per unit effort (CPUE) will be influenced by the abundance of fish in neighboring populations and therefore CPUE may provide a poor index of local abundance. I found evidence for competition among vessels in data from a British Columbian trawl fishery, although the underlying mechanism was unclear. Also, as predicted by the IFD, CPUE was on average equalized among the areas of this fishery.

Diet choice theory, the methodology of dynamic programming, and data from the sablefish (*Anaplopoma fimbria*) component of the Oregon trawl fishery were used to develop a model to identify the conditions that would lead to high-grading behavior at sea. The results of the model indicated that trip duration, trip quota, risk, and fish availability influenced high-grading through their effect on the probability of exceeding the allowable catch. Greater discarding at the end of trips and when fish availability was high was observed in the data, as predicted by the model. In a simulated fishery based upon this model, the regulation of trip durations and trip quotas were compared by their effects on several indicators such as high-grading, expected economic value of

a trip, proportion of a trip quota filled, and number of trips in a season. Intermediate trip lengths and large trip quotas best satisfied the multiple goals typically used by management agencies.

## **Dedication**

To my father, who can not see it, and my mother, who has borne much to see it  
completed.

## Quotation

Break, Break, Break

On thy cold gray stones, O Sea!

And I would that my tongue could utter

The thoughts that arise in me.

Oh well for the fisherman's boy,

That shouts with his sister at play!

Oh well for the sailor lad,

That he sings in his boat on the bay!

And the stately ships go on

To their haven under the hill;

But Oh for the touch of a vanished hand,

And the sound of a voice that is still.

Break, Break, Break

Alfred, Lord Tennyson, 1842

Stanzas 1-3.

## Acknowledgments

Though the contents of this thesis are ultimately my responsibility, the ideas and work presented here would not have been possible without the interaction, support and assistance of numerous individuals. At Simon Fraser University L.M. Dill generously provided me with space, time, and encouragement, even though I was never formally a member of his laboratory. C.W. Clark (from the University of British Columbia) allowed me to audit the dynamic programming course that he taught at Simon Fraser University, which provided the methodology for the third and fourth chapters of this thesis. The members of the Behavioral Ecology Research Group and of the Fisheries Discussion Group from the Resource and Environmental Management Program at Simon Fraser University have made numerous contributions to this work through informal discussions and formal seminars. The assistance and support of M.F. Lapointe were especially appreciated. As well as intellectual support, D.M. Hugie also provided the computer that the final version of this thesis was produced upon. In addition to my senior supervisor, R.M. Peterman, many people improved the quality of this work by reviewing various sections of this thesis in earlier forms, greatly improving the final quality of this work. These people were M.V. Abrahams, D. Boullion, R.N. Crittenden, L.M. Dill, L.S. Forbes, M.F. Lapointe, M. McAllister, D. Soluk, A.V. Tyler, and R.C. Ydenberg. K.E. Reis assisted me with the final proof-reading of the thesis. Finally, J.M. Emlen and E.K. Pikitch provided me with useful discussions and suggestions as well as a place to stay when I was working in Seattle.

Many people involved with the fisheries of British Columbia made significant contributions to this work, through discussions and by providing opportunities to observe commercial fishing operations. I am particularly indebted to the captain and crew of the FPV Tanu and the FV Freeport, as well as D. March (Deep Sea Trawler's Association) and N. Venables (liaison officer, Fisheries and Oceans, Canada).



The data used in this thesis were the result of the efforts of earlier workers and they must share the credit for any successes that I have had. Fisheries and Oceans, Canada provided the data for the analysis in the third chapter, based upon many years of collection by their staff. In particular, A.V. Tyler, J. Fargo and R. Foucher, from the Pacific Biological Station, Nanaimo, B.C., assisted in the data retrieval. E.K. Pikitch provided access to the data, from her Oregon trawl fleet observer study, that I use in the third and fourth chapters. D. Erickson coordinated the observer study and J. Wallace organized and maintained the data base from the study.

Financially, my research was supported by an NSERC scholarship, graduate student research fellowships from Simon Fraser University, a research contract from the Department of Fisheries and Oceans, and an NSERC grant to R.M. Peterman.

Finally, I would like to acknowledge the members of my supervisory committee for their support throughout my thesis, which has often exceeded their obligations to me as a graduate student.

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## Preface

This thesis was written as a series of papers for submission to refereed journals in the fields of fisheries and behavioral ecology. The second chapter has already been accepted for publication in the Canadian Journal of Fisheries and Aquatic Sciences. The third chapter will be submitted to Behavioral Ecology and the fourth chapter will be submitted to the Canadian Journal of Fisheries and Aquatic Sciences. A number of minor alterations have been performed to join these three chapters (chapters 2-4) into a thesis. The text of these chapters has been preceded by an introductory chapter describing the common philosophy that unites them as a single work, and followed by a concluding chapter summarizing their significance. Also, the numbering of all pages, tables, and figures in the chapters has been altered to run consecutively throughout the thesis. Finally, the references have been collected into a single bibliography at the end of the thesis, following the format of the Canadian Journal of Fisheries and Aquatic Sciences.

## Chapter 1

## General Introduction

Currently, there is little formal theory about how the decisions made by individual fishermen will affect the mortality rates experienced by populations of fish due to commercial harvesting. Hilborn (1985) stated "Most fisheries problems arise from a failure to understand and manage fishermen, and ... the study of fishermen should be a major part of fisheries research." Though much work has been performed by economists to study patterns of investment by fishermen and the fishing industry (e.g. Charles 1989, Clark 1985, Lane 1988) comparatively little work has been done on decisions made by fishermen at sea, such as the choice of where to fish (but see Hilborn and Ledbetter 1979, Eales and Wilen 1986) or which fish to keep from a catch (but see Pikitch 1987). These decisions that are made by fishermen during fishing activities are the focus of this thesis.

Foraging theory, from behavioral ecology (Krebs and Davies 1984), provides a rich theoretical framework to examine questions such as what, where, and when to hunt, as applied to non-human foragers. In that field, economic models of individual behavior are based upon the assumption that animals make decisions in order to maximize their genetic contribution to future generations (fitness) through the maximization of some proximate currency such as energy gain or survival (Stephens and Krebs 1986). These models have provided hypotheses that have withstood testing in situations as diverse as the choice of diet by small birds (Krebs et al. 1977), choice of feeding site by fish (Abrahams and Dill 1989, Gillis and Kramer 1987, Godin and Keenleyside 1984), and choice of optimal group size in carnivores (Clark 1987, Giraldeau and Gillis 1988).

Foraging theory has been successfully adopted by some anthropologists in their effort to explain patterns in human foraging (see Foley 1985, Smith 1983 for reviews). Though the complexities of human societies make the application of evolutionary



paradigms potentially more complex than in the case of other foragers, the goal of maximizing fitness can be applied to human foraging decisions when the relevant proximate currencies are either assumed or identified. For artisanal foragers these currencies may be calories, protein, or some combination of nutrients required for survival (e.g. Hill 1988). In industrial societies, such as ours, the monetary value of a food item may indicate its value to members of the society. However, it is unlikely that monetary currencies provide a complete description of the underlying value of the alternative decisions that people face; economists have recognized this with the development of utility theory (Keeney and Raiffa 1976). Still, monetary currencies provide a parsimonious starting point for studying the decisions faced by commercial fishermen at sea.

The central proposition of this thesis is that foraging theory provides a source of relevant and testable hypotheses for use in the study of human fishing activities that can result in new insights into the relationship between fishing activities and fishing statistics. The magnitude of fishing activities is defined as fishing effort and is measured by enumerating the number of vessels, the quantity of fishing gear deployed, or the time spent performing particular tasks at sea over a fixed period of time (Ricker 1975). The fishing statistics commonly collected from commercial fisheries are usually based upon the landed catch and the expended effort reported by the fishermen at the end of their trips. In the following chapters, I will show that catch and effort data from commercial fisheries will differ from the data desired by researchers because the goals of commercial fishing are based upon maximizing fishermen's benefits rather than maximizing information about the fishery.

In the second chapter, I use the ideal free distribution (IFD, Fretwell and Lucas 1970) to develop hypotheses tests that relate the spatial distribution of fishing effort to local differences in catch rates. This chapter identifies the conditions necessary for IFD theory to apply to a fishery, develops a methodology to test for these conditions using

the catch and effort data that are available, and discusses the implications that the IFD could have for the estimation of fish abundance from fishing statistics.

In the third and fourth chapters the focus changes to another aspect of fishing effort that has previously received little theoretical attention: the discarding of the less valuable but potentially marketable fish at sea (high-grading). Discarded fish are not easily enumerated in estimates of the catch and the fish discarded from trawl fisheries usually do not survive (Saila 1983). Thus, discarding represents a loss of present and future revenue from a fishery. Also, the unreported mortality that results from discarding causes underestimates of fishing mortality which bias stock assessments that are based on landing statistics.

In the third chapter a state- and time-dependent model of high-grading behavior is developed using stochastic dynamic programming (Mangel and Clark 1988). The goal of this model is to predict how high-grading behavior will vary with the amount of fish that can be landed, the availability of fish, and the risk that a fishing trip will end prematurely due to injury or gear damage. The model is developed for the sablefish (*Anaplopoma fimbria*) component of the Oregon trawl fishery and the patterns of discarding generated by the model were compared to the patterns observed in that fishery.

Management agencies have recently begun to consider implementing limits on the amount of effort expended during a fishing trip and the amount of fish that can be landed from a trip. However, such regulations could lead to high-grading that would result in biased catch estimates and additional unreported fishing mortality. In the fourth chapter, I expand the analysis of the dynamic programming model to examine how the amount of high-grading behavior in a fishery could be affected by management regulations limiting the duration of a trip and the amount of fish that can be landed from each trip when the total amount of fish landed by all trips during a season remains constant. This model quantifies the effect of varying management regulations on

several variables that are relevant to fishermen and managers including the amount of fish that is discarded, the number of trips in a season, the value of the landed catch from a trip, and the duration of a trip.

Each of these three chapters is concerned with current issues in commercial fisheries: the interpretation of catch and effort statistics in the second chapter and discarding of fish at sea in the third and fourth chapters. Furthermore, each of these chapters contributes to the view that the decisions made by fishermen at sea are of major importance to current issues in commercial fisheries.

## **Chapter 2            The application of the ideal free distribution to the spatial allocation of effort**

### **Introduction**

The relationships between catch and fishing effort are known to be complex and not simply governed by fish abundance (Paloheimo and Dickie 1964; Rothschild 1977; Clark and Mangel 1979). Yet, in lieu of better information, catch per unit effort (CPUE) remains a common index of abundance in many fisheries. It is used either as a direct indicator of abundance (Hayman et al. 1980; Cooke 1985) or as a means of fine tuning other stock assessment techniques (Deriso et al. 1985). However, the spatial and temporal distribution of effort for a commercial fishing fleet is not the same as for a research survey. Fishing is non-random in a fleet, with effort allocated to maximize benefits to the fishermen rather than to maximize information about the distribution and abundance of fish (e.g. Cook 1984). Thus, CPUE will be influenced by both fish abundance and behavior of fishermen. In spite of the wide use of CPUE, until recently little work has been directed toward understanding how the movement dynamics of fishing fleets affect the interpretation of fisheries statistics.

The recognition of fishermen as responsive components in the fisheries system has led to the formal study of "fleet dynamics". Hilborn (1985) categorized these studies of fishing effort into four areas: 1) investment and fleet size, 2) effort allocation (spatial and temporal), 3) harvest efficiency, and 4) discarding and by-catch. Previous workers have taken approaches to understanding fleet dynamics varying from qualitative anthropological observations (Andersen 1973; McCay 1978) to simulation modeling of the behavior of fishermen (Smith et al. 1982; Allen and McGlade 1986). Quantitative studies of causal relationships among the components of specific fisheries are also becoming more common (Millington 1984; Smith and McKelvey 1986; Lane

1989; Lapointe 1989, Abrahams and Healey 1990). My study contributes to this latter group by focusing on the effect of changes in CPUE on the spatial distribution of fishing effort. Vessel movements among areas in response to local changes in CPUE have been documented in a salmon seine fishery (Hilborn and Ledbetter 1979) and a shrimp trawl fishery (Eales and Wilen 1986). However, the hypothesis tests in those studies were based on the knowledge of specific situations rather than on an attempt to understand vessel actions using a more general set of theories about spatial dynamics of searching predators. Behavioral ecology (Krebs and Davies 1984) provides such an appropriate set of theories, based upon the optimization of a single currency (net value of the catch), which allow us to hypothesize relationships between distributions of foragers (units of fishing effort) and the availability of resources (fish distribution and abundance).

#### The Ideal Free Distribution

In this study of the movement dynamics of fishing vessels, I used the ideal free distribution (IFD, Fretwell and Lucas 1970, Fretwell 1972), a simple and robust hypothesis from behavioral ecology that provides the rationale for making predictions about the distribution of foragers. When resources are distributed among a number of distinct areas and when foragers must choose among those areas, the IFD predicts the equilibrium number of foragers in each area based upon several assumptions. Two of these assumptions are ideal knowledge of the environment and free movement among areas. Ideal knowledge refers to knowledge about both the distribution of the resource among areas and the distribution of other foragers. Free movement refers to the ability to change areas without restrictions or travel costs. In addition, this theory assumes that competition among foragers occurs in proportion to their local density and that foragers have equal competitive abilities. This form of interference competition (Goss-Custard 1980) implies that competitive costs (such as reduction in foraging rate) are

rapidly reversible, and track predator density. Interference competition is distinct from exploitation competition, where the impact of competition will still be felt after the competitor density drops because of reduced resources. There are other assumptions, but these are the most relevant ones for my study. Under these circumstances, the IFD predicts that the profit rate for an individual in an area will be proportional to the availability of resources divided by the number of individuals foraging there. When each forager is free to move so as to maximize its own profitability, the result is an equilibrium distribution where foragers in different spatial areas have the same profit rate. As a result of this equalization of profit rate, the number of foragers in each area will reflect the abundance of resources better than profit rate. If the ideal free distribution applies to a commercial fishery, then I would expect that boats would move among fishing areas so as to adjust competition to the point where CPUE would be the same in all areas.

In spite of the oversimplifying nature of its assumptions, the IFD has led to useful tests of hypotheses in field and laboratory studies. In the case of non-human foragers, the results often agreed with the IFD predictions even when some of the IFD's assumptions were violated (Whitham 1980; Harper 1982; Godin and Keenlyside 1984; Talbot and Kramer 1986; Gillis and Kramer 1987; Abrahams and Dill 1989; see Milinski and Parker 1991 for review). Those results illustrate the robust nature of the IFD and suggest that it is a good first model for approaching the study of fisheries situations involving numerous foragers moving among spatial locations.

### Purpose

The purpose of my study was to assess the applicability of the IFD to the trawl fishery in the Hecate Strait, British Columbia, Canada, by testing the assumptions and a prediction of the IFD using historical catch and effort data. My work differs from previous IFD studies because the spatial distribution of foragers was compared with

foraging success (measured as CPUE) rather than comparing that distribution to the underlying spatial distribution of resources. This was necessary because the fishery data obtained from the Canada Department of Fisheries and Oceans did not contain estimates of local fish abundance that were independent of fishing, but they did provide data on the foraging success of individuals. As shown below this is actually appropriate for my purpose because fishermen's perceptions of the relative abundance or availability of fish are at least partially influenced by CPUE. Also, my work differs from previous studies of fleet dynamics by applying an existing, general ecological foraging theory to a fishery, with the goal of predicting the spatial distribution of fishing effort. I chose to apply the IFD to existing catch and effort data, rather than collecting new data, in order to develop a methodology that could be readily applied to other fisheries without significant additional costs.

When applied to a fishery, the IFD could lead to predictions of the spatial responses of effort to changes in fish abundance or management plans. For example, if a stock collapse were occurring in some area, the resulting spatial redistribution of fishing effort among the remaining stocks could be predicted. Also, the effect of a change in fleet size on the spatial distribution of effort could be anticipated before regulations were altered. In general, a mechanistic, testable model of the spatial allocation of effort would allow fishery managers to quantify the potential reactions of a fleet to changes in the distribution, abundance, or access to fish.

I also took a simpler approach to compare with my IFD analysis. That simpler approach correlated local fishing effort with local CPUE values, following previous work by Argue et. al. (1983) and Lapointe (1989). This analysis was based on the "local response" hypothesis that the changes in the amount of fishing effort expended in an area only follow changes in the CPUE of that area. This method thus assumes that the ideal free distribution does not apply because it does not take into account the effect of fishing success in other areas on movement of effort among areas.

## Methods

I studied the bottom trawl fishery in the Hecate Strait, located between mainland British Columbia and the Queen Charlotte Islands (Fig. 1). Three data sets were used. The main data set was the landings data base (Groundfish Select files) provided by the Canada Department of Fisheries and Oceans in Nanaimo, B.C. These data come from landings reported by fishing vessels at the end of each trip. I focused on trips that targeted on Pacific cod (*Gadus macrocephalus*) and the associated species, English sole (*Parophrys vetulus*), Dover sole (*Microstomus pacificus*), rock sole (*Lepidopsetta bilineata*) or lingcod (*Ophiodon elongatus*). This limited the analysis to vessels fishing in the same local areas and depths with similar gear. The years 1976 through 1979 were selected for this work, because they are years with complete data and relatively high fish abundance.

I also used data from 1976 through 1979 sales slip information and the consumer price index (CPI, Statistics Canada 1980). The sales slip data base contains the prices paid for all species landed. With this information I converted the weights of the fish landed to dollar values. I then used the CPI to adjust these dollar values to standard 1971 dollars, which is the base year for the CPI. Based on the CPI, \$100.00 in 1971 had the purchasing power of \$26.59 in 1990 (Statistics Canada 1982, 1991). Because data on trip costs were not available, I used these gross profit estimates in my analysis as the best available approximation of the net profit for the trip.

The available data enabled me to test two of the four assumptions of the IFD noted above, that movement of foragers among areas occurs and that competition among foragers exists. These two conditions are required for an IFD to be applicable. I could not determine from the available data whether that movement was "free" but costs of moving among areas are undoubtedly not negligible. Furthermore, again because of lack of data, I could not test the "ideal knowledge" assumption or the assumption that the competitive abilities of all vessels in the fleet were equal.



However, this was not a serious problem because as I noted in the Introduction, the predictions of the IFD are often robust to violations of its assumptions, particularly the generally unrealistic ones such as ideal knowledge and movement without costs. Additionally, cooperative fishing strategies and informal social interactions among fishermen (e.g. Orbach 1977) could increase the transmission rate of information through the fleet and give each individual a more "ideal" knowledge of the current distribution of fish.

I could not test the main IFD prediction of equality of CPUE among all foragers because of restrictions in the availability of data. In order to maintain confidentiality, the Department of Fisheries and Oceans could only provide records of trips, without identifying the vessels that made each trip. However, if the main prediction of equality of CPUE among vessels is true, then a derived prediction would be that mean CPUE values in each area should be equal at any one time. I was able to test this derived hypothesis with the available data, as described below under "Equalization of CPUE".

Before addressing the role of the IFD in the Hecate Strait fishery, I summarized the general characteristics of trips for the four years studied. The data used for this step contained information for each trip on the date that the trip ended, the duration of the trip, the time spent fishing (effort, in hours with nets in the water), the areas visited, and the CPI-adjusted value of the catch; the latter was the sum of the value of all species landed. In addition, CPUE (landed value/time fishing) and the proportion of time fishing (time fishing/trip length) were also calculated. Finally, the average fleet size experienced during each trip was defined as the mean of the number of simultaneous trips occurring per day during each day of the trip.

#### Movement of Vessels Among Areas

The initial analysis focused on the statistical areas used for following the spatial dynamics of fishing effort. The statistical reporting areas defined by the Department of

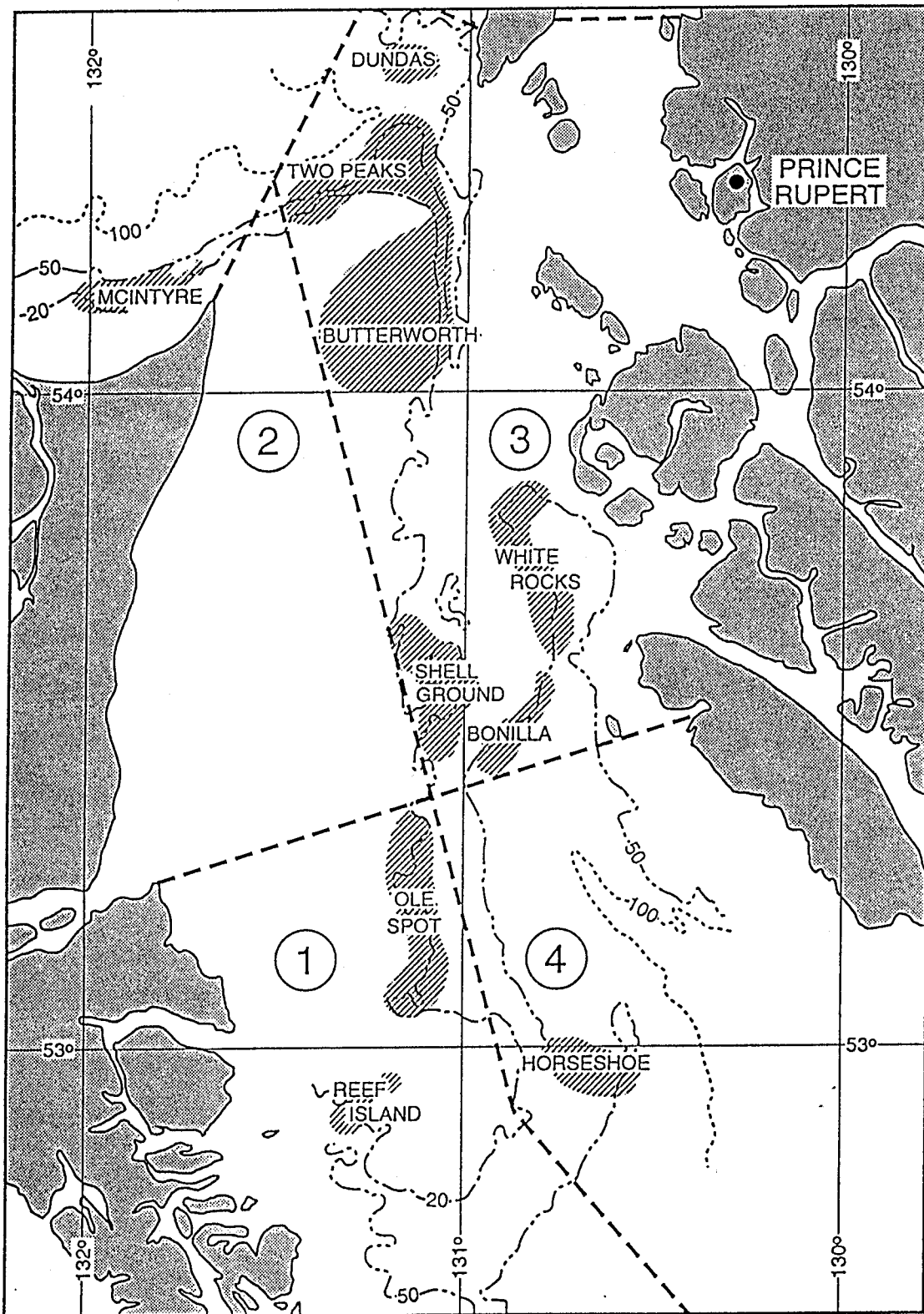
Fisheries and Oceans are illustrated in Figure 1. In order to determine if the movement assumption of the IFD was reasonable in this fishery, I wanted to know if vessels were fishing in all areas studied and whether vessels were visiting more than one area in a trip. In addition, I looked for preference in trips visiting only one area or seasonal patterns in use of areas.

### Aggregation of Data

The remaining analyses focused on the prediction of spatial allocation of effort using information from individual trips that had been grouped into statistical areas and weeks (a week was the average duration of a trip during the years studied). Thus, the experimental unit for these remaining analyses was changed from a trip to the activity within a statistical area during a single week. I used 7-day standard weeks beginning on January 1, 1976. When a trip overlapped more than one week, the effort and catch of the trip was allocated among the adjacent weeks according to the proportion of the trip's duration occurring in them. Thus, if a 14-day trip in an area overlapped three standard weeks, with 3 days in the first week,  $3/14^{\text{ths}}$  of the entire trip's catch and effort would be added to the first week's total catch and effort for that area. Similar assumptions were not required to allocate data among areas because boats that visited more than one area reported catch and effort separately for each area fished.

My manner of analyzing the aggregated data assumes that the effort and catch values used are independent among weeks. This seems unlikely to be absolutely true, given my methods of aggregation and the potential for decisions in one week to influence the distribution of effort in the following week. However, no test for independence in the catch and effort time series will be free of the confounding effect of autocorrelation in the unknown, underlying distribution of fish. In fact, a weekly interval likely provides adequate opportunity for the potential redistribution of effort, and my data below suggest that it is the most appropriate time scale for my study.

Figure 1. A map of Hecate Strait, which lies between the Queen Charlotte Islands and the northern coastal mainland of British Columbia. Numbered areas are the statistical reporting areas used in this study. Fishing grounds are indicated by cross-hatched regions (modified from Westrheim 1983).



## Tests for Competition

The aggregated data set was used to test for the existence of competition among foragers (fishing vessels), which is a necessary condition for the presence of an IFD. I defined competition as an interaction among foragers that results in a decrease in foraging rate (CPUE) associated with an increase in number of foragers. I tested for competition by comparing the change in effort between weeks for an area with the corresponding change in CPUE in the same area. Though effort may change without variation in vessel density, if fishing time is being maximized at sea, there will be a strong correlation between the two variables. Competition would be indicated if CPUE tended to decrease during weeks when effort increased or if CPUE tended to increase during weeks when effort decreased. If fish abundance were constant across weeks, I would expect CPUE to decrease as effort increased. The comparison between the changes in CPUE values between weeks of increasing and decreasing effort was made using the Mann-Whitney U test due to the distribution of the data, which did not permit the use of a parametric test.

## Equalization of CPUE: Proportional Regressions

Previous workers (Hilborn and Ledbetter 1979, Millington 1984, Lapointe 1989, Hilborn and Kennedy in prep.) focused their studies on the ratio of CPUE within an area to the average CPUE among all areas. They hypothesized that this ratio would remain constant through time and would reflect the relative costs of fishing in each area. As well, if CPUE and costs were equal in all areas, then this ratio would equal one. However, this model implicitly assumes a particular cost structure that may not apply to my fishery. Instead, I tested for the equality of CPUE among areas by regressing the proportion of total Hecate Strait catch in each area within each week on the proportion of total Hecate Strait effort in the same area during the same week. If effort is allocated among areas so that CPUE is equalized among areas, then, when  $C_i$

and  $f_i$  are the catch and effort in area  $i$  for a particular week:

$$(1) \quad C_i/f_i = \Sigma C_i/\Sigma f_i = R,$$

where  $R$  is the ratio, or CPUE value that is equalized among all areas in the week being considered. By rearrangement then,

$$(2) \quad C_i/\Sigma C_i = f_i/\Sigma f_i$$

This is in the general form of a linear regression  $Y = aX + b$ , where  $a=1$  and  $b=0$ . Thus, if the IFD applies, the regression of the proportion of catch in area  $i$  on the proportion of effort in area  $i$  (equation 2) will be a line with an intercept of zero and a slope of one. If the IFD holds, all points will fall on this line, regardless of the weekly values of  $R$ . Also, this relationship should hold for all data combined as well as any subsets of the data. Subsets of the data were tested in order to determine if some of the observed variation around the line could be attributed to area-specific effects or seasonal effects.

### Local Response Hypothesis

I also examined the temporal dynamics of effort in each area and for the whole Strait by assuming that effort responded to local changes in CPUE without regard for CPUE in neighboring areas (unlike the IFD theory). This "local response" approach follows from earlier work by Argue et al. (1983) and Lapointe (1989) and is a simple alternative to using the IFD in order to predict the spatial distribution of effort among areas. I would expect effort to be closely related to CPUE (or some lagged value) when the area considered encompassed most of the regions fished by the fleet, or if some subset of the fleet fished exclusively in the area. Specifically, I tested the

Spearman rank correlations between effort and 1) CPUE for the present week or 2) the CPUE of each of the 4 previous weeks for each area. These various lags tested for a delay in the acquisition of information about fishing success in the areas. I also performed the same analysis on the effort and CPUE values for the entire Hecate Strait in order to test for a relationship between CPUE and total fleet effort.

The null model implicit in these correlations is that the effort in each area is independent of the CPUE for that area at any lag. Another null model that could be postulated is that effort is independent of catch alone. When the latter null model is true, a spurious negative correlation occurs between CPUE and effort (Roff and Fairbairn 1980). However, neither null model will generate a positive correlation between CPUE and effort, which is what I expect to see if effort is being attracted to areas where fishing is more successful, as postulated by the local response hypothesis.

#### Statistical Considerations

I performed many hypothesis tests in groups, with stratified data sets or with several time lags being considered simultaneously. Given this large number of tests, in order to more accurately represent the probability of type I statistical error, sequential Bonferroni comparisons (Rice 1989) were used at a 0.05 group-wide  $\alpha$  level. This means that the actual  $\alpha$  value used for a test varied between 0.05 and  $0.05/n$  ( $n$  = the number of simultaneous tests) within a group of tests.

When possible, in those cases where I failed to reject the null hypothesis, I calculated statistical power (the probability that I could have correctly rejected the null hypothesis with my sample if it was false at some specified effect size, Dixon and Massey 1969). I calculated power for  $\alpha=0.05$  in all tests in order to facilitate comparisons among them.

## Results

Table 1 summarizes the characteristics of groundfish landings from the Hecate Strait during 1976-1979. Because of the highly skewed nature of some of these data, I report the mean, median, 25th and 75th percentiles. The median and mean trip length were almost the same; they were both about one week in duration. This typical trip length was the basis for my choice of a one-week time interval to study spatial allocation of effort. An average of 14% of the total trip time was spent fishing (with nets in the water). Time fishing and effort did not include the time spent moving among fishing sites or handling the fish after they were brought on board.

### Movement of Vessels Among Areas

The fleet distributed itself among all of the defined statistical areas except area 2 (Table 2). This area had no suitable sites for catching the species that I focused on, and therefore it was dropped from subsequent analyses. In some cases all areas were visited within a single trip (Table 2). However, the use of the areas clearly was not uniform. Most trips involved visits to only one area. Even among the trips visiting only one area, the distribution of trips among the areas was not random (Chi-square=32.3, d.f.=2,  $P < 0.001$ ). The majority of the trips occurred in area 3, which was the closest area to the port of Prince Rupert (Fig. 1).

The strategies of area use varied seasonally (Chi-square=80.6, d.f.=18,  $P < 0.001$ ). Summer and fall (June - November) trips tended to concentrate around Prince Rupert more than the spring and winter trips (December - May) (Table 2). Trips were also more numerous during summer and fall, when weather conditions are generally less severe than other months (Thompson 1981).



Table 1. A summary of trip characteristics based on landings data from the Hecate Strait trawl fishery that targeted on Pacific cod and associated species for 1976-1979. The mean, median, 25th and 75th percentiles were calculated to the nearest integer value from all reported trips. Effort is defined as time fishing in hours. Catch is the CPI-adjusted value of all species landed in a trip.

Characteristic	Mean	Median	P <sub>25</sub>	P <sub>75</sub>
Fleet Size (vessels)	10	10	8	13
Trip Length (h)	176	168	120	216
Fishing Time (%)	14	11	5	20
Effort (h)	22	18	8	32
Catch (\$)	17544	10515	4421	20925
CPUE (\$/h)	1836	534	242	1372

Table 2. Total and seasonal area usage by individual vessels during 1976-1979. The table summarizes the number of trips to each area and all combinations of areas. Area 2 does not appear because no trips were targeted on the relevant species in this area.

Areas Fished	Number of Trips				
	All	Spring	Summer	Fall	Winter
3	216	31	88	68	29
4	134	19	31	57	27
1	124	23	64	18	19
1&4	101	30	20	30	21
3&4	73	20	13	17	23
1&3	54	13	25	12	4
1&3&4	50	10	18	13	9
Total	752	146	259	215	132

## Tests for Competition

There was an inverse relationship between changes in effort within an area and the corresponding changes in CPUE in that area (Table 3), which suggests that there was competition among fishing boats. Increases in effort during a week were associated with decreases in CPUE, while decreases in effort were associated with an increasing CPUE. This trend was significant for all data combined, for area 3 alone when the analysis was done for each area separately, and for the spring when the analysis was done seasonally. Area 3 was the area with the greatest fishing activity during the study period (Table 2), but it was also the area with the largest number of fishing grounds (Fig. 1). The concentration of effort within a few of the available fishing grounds at any one time may have been the cause of the statistically significant tests for competition in this area. The significant spring result suggests that this is a time of year when vessel competition is exceptionally strong. My failure to detect competition in other spatial and seasonal subsets of the data was not conclusive because the statistical power of the Mann-Whitney U test cannot be determined for non-normal, heteroscedastic data like mine (though its power is close to that of a t-test when data are normal and homoscedastic, Seigel 1956).

I was unable to test statistically for the mechanism underlying the observed competitive patterns in the data. Discerning between exploitation and interference was beyond the resolution of my data.

## Equalization of CPUE: Proportional Regressions

The linear regression of the proportion of the weekly catch in an area on the proportion of weekly effort in that area provided a reasonable fit to the observed data (Fig. 2, Table 4). The significance tests associated with linear regression are robust to deviations from normality in the error terms when the distribution of the regressor variable is approximately normal (Box and Watson 1962). An examination of the

Table 3. Tests for competitive effects in catch-effort data. The Mann-Whitney U test was used to compare changes in CPUE associated with increases or decreases in effort for an area. If increased effort has a more negative change in CPUE than decreased effort, then there is evidence for competition. The test results are given for this one-tailed hypothesis. The values in parentheses are the number of cases in the category. U = Mann-Whitney U statistic, N = total sample size, P = probability of being wrong if the null hypothesis of no association between changes in effort and changes in CPUE is rejected. Data were analyzed using sequential Bonferroni comparisons and a 0.05 group-wide significance level. \* Indicates significant with that adjusted significance level.

Table 3

<b><u>Breakdown</u></b>	Mean Change in CPUE (\$/h)		U	N	P
	for	for			
	Increased Effort	Decreased Effort			
<b><u>All</u></b>	-205 (268)	+198 (251)	29355	519	0.006*
<b><u>Area</u></b>					
1	-49 (87)	+113 (80)	3480	167	0.5
3	-207 (95)	+228 (75)	2546	170	0.001*
4	-307 (83)	+252 (94)	3515	177	0.128
<b><u>Season</u></b>					
Spring	-700 (56)	+616 (41)	832	97	0.011*
Summer	-49 (84)	+73 (79)	3214	163	0.365
Fall	-105 (78)	+136 (79)	2604	157	0.047
Winter	-73 (50)	+151 (52)	1175	102	0.201

transformed proportional effort values revealed a nearly bell-shaped distribution. Therefore, I used linear regression as the statistical model for my hypothesis tests about the equalization of CPUE among areas.

When the data from all four years were combined, there was a significant difference between the observed slope and the slope of 1.0 that was predicted by the IFD (Table 4). However, the actual difference was small (observed slope=0.943). Figure 2 shows graphically that the predicted and observed lines were similar. In addition, the slopes of all regressions in Table 4 are close to the IFD prediction even when they are statistically different from it due in part to the large sample sizes (slopes are between 0.9 and 1.1 in 6 of the 8 regressions in Table 4). This indicates that CPUE tended to be equalized among areas fished as predicted by the IFD, even though some deviation from the prediction occurred.

None of the regressions of the proportion of catch on the proportion of effort differed significantly from the IFD prediction when the data were analyzed separately for each area (Table 4), yet in each case there was a power of at least 0.89 to detect a difference of 0.2 from a slope of one at  $\alpha=0.05$ . The r-squared values of these regressions varied from 0.56 to 0.77, with the lowest value occurring in area 3 and the highest value in area 4. The r-squared values were greatest when the number of fishing grounds in an area were fewest (Fig. 1). This pattern in r-squared values may have been the result of the spatial scale of data collection (statistical reporting areas), which was larger than the scale of vessel movements (fishing grounds), and which allowed a greater potential for variability in the relationship between the proportional catch and the proportional effort than if the data had been collected by fishing ground.

In the seasonal breakdown of the analysis, the slopes differed significantly from 1 in both the summer (June - August) and winter data (December - February) (Table 4). In the summer, the observed slope was greater than one. This trend suggests that areas with high relative effort have a greater catch than would be predicted by the IFD. In

Figure 2. A test for equality of CPUE using proportional effort and proportional catch. The proportions are calculated among the areas fished for each week and all proportions are arcsin transformed. The dashed line indicates the relationship predicted by the IFD, and the solid line is the least squares regression line for the data ( $r^2=66.9$ , slope=0.943).

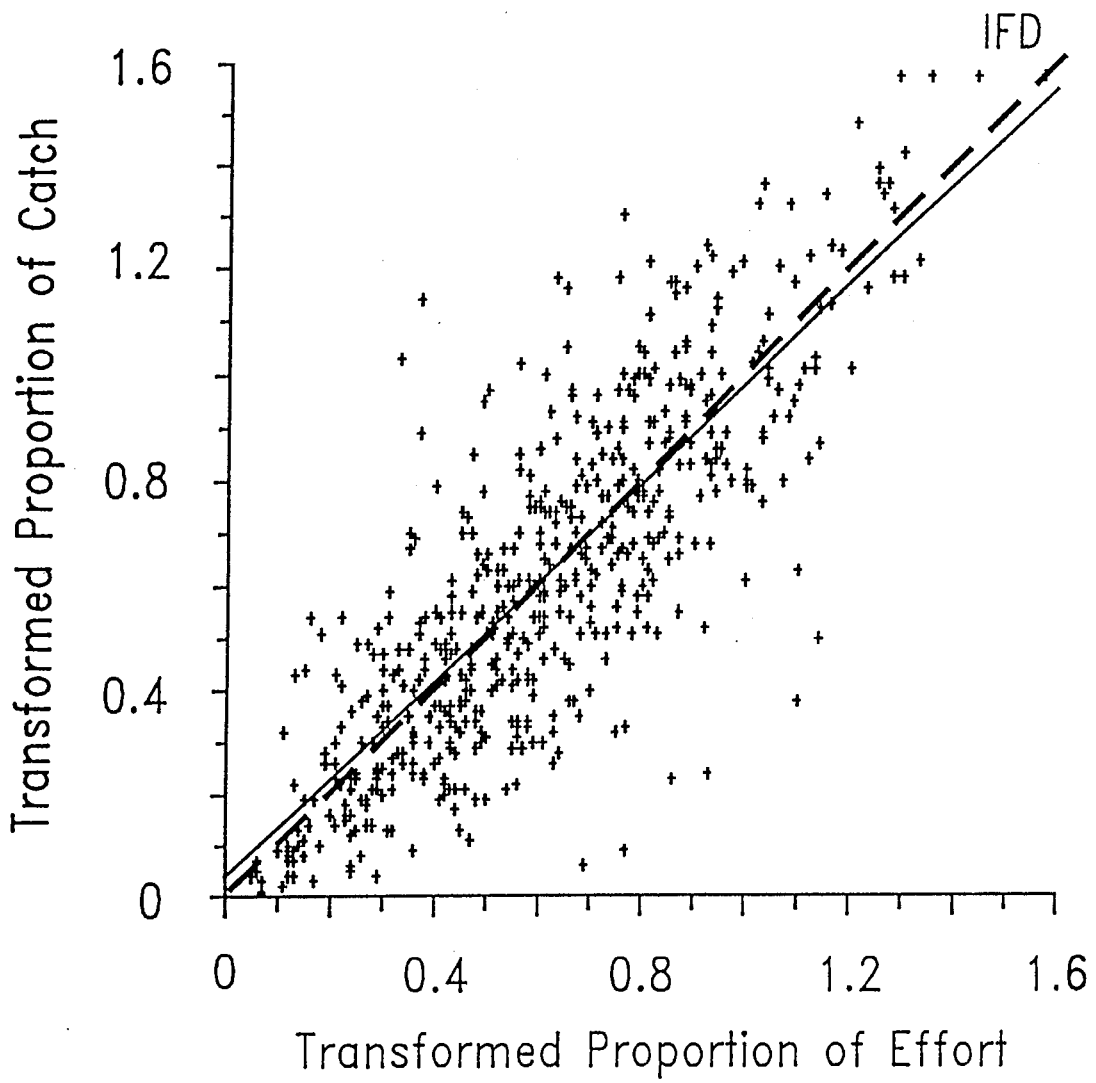




Table 4. Tests for the equality of CPUE among areas. Equalized CPUE is indicated by a slope (b) of 1 in the regression of proportional catch on proportional effort (eqn. 2). The estimated slopes were compared to 1.0 with a two-tailed t-test.  $r^2$  is the coefficient of determination and N is the sample size. All proportions were arc-sin transformed. The analysis was performed on all of the data combined, and for spatial and seasonal subsets of the data. The hypotheses were analyzed using sequential Bonferroni comparisons and a 0.05 group-wide significance level applied to the spatial and seasonal breakdowns of the data. The power to detect a value different from 1.0 is shown for a value of the parameter that differs from 1.0 by 0.2 (effect size,  $d=0.20$ ). All power values were calculated for  $\alpha=0.05$ . Power is not applicable (N.A.) when the null hypothesis was rejected.

Table 4

	$r^2$	b (S.E.)	N	P	Power (d=0.20)
<b><u>All data</u></b>	0.669	0.943 (0.028)	546	0.044*	N.A.
<b><u>Spatial Breakdown</u></b>					
1	0.617	0.948 (0.056)	180	0.315	0.991
3	0.560	0.937 (0.062)	179	0.324	0.896
4	0.774	1.0 (0.040)	187	>0.9	>0.995
<b><u>Seasonal Breakdown</u></b>					
Spring	0.665	0.925 (0.060)	105	0.214	0.912
Summer	0.695	1.148 (0.059)	163	0.005*	N.A.
Fall	0.669	0.907 (0.052)	162	0.068	0.952
Winter	0.682	0.812 (0.052)	116	<0.001*	N.A.

Table 5. Tests of the local response hypothesis. Spearman rank correlations ( $r_s$ ) between fleet effort (hours fished) and CPUE (\$/h fished) for different weekly time lags. Results are given for the entire Hecate Strait and each area separately. N is the sample size. The 5 lag tests for all areas combined and each area individually were analyzed using sequential Bonferroni comparisons and a 0.05 group-wide significance level. \* Indicates significant with that adjusted significance level.

Area		Lag (weeks)				
		0	1	2	3	4
All	$r_s$	0.034	0.237	0.232	0.088	-0.047
	P	0.318	<0.001*	<0.001*	0.125	0.274
	N	192	174	170	172	165
1	$r_s$	0.221	0.311	0.389	0.306	0.196
	P	<0.001*	<0.001*	<0.001*	<0.001*	0.009*
	N	180	154	154	156	147
3	$r_s$	0.113	0.467	0.256	-0.016	-0.269
	P	0.038	<0.001*	<0.001*	0.424	<0.001*
	N	179	151	147	156	143
4	$r_s$	-0.133	-0.157	-0.110	-0.223	-0.183
	P	0.034	0.022	0.082	0.002*	0.011*
	N	187	165	161	163	158

contrast, the winter months had a slope that was less than one, indicating a tendency for an area to have lower CPUE than would have been predicted by the IFD when the proportional effort values are high. These slopes suggest that vessels are aggregating beyond a level that can be attributed to the distribution of the fish during the winter months and overdispersing in the summer months, so that they are more evenly distributed than the fish.

### Local Response Hypothesis

Tests of the hypothesis that effort allocation can be related to local CPUE, regardless of CPUE in other areas, yielded ambiguous results (Table 5). The total effort in all areas combined was positively correlated with CPUE lagged for one and two weeks, as I would expect if the fleet fished mostly in the Hecate Strait for the species considered. However, when the data were stratified by statistical area, the results were less clear. Area 1 had positive correlations between total effort and all CPUE lags studied, from 0 to 4 weeks. In contrast, in area 4 there were negative correlations between effort and CPUE that were significant for 3 and 4 week lags. The seasonal breakdown of the analysis within areas was no clearer and I do not include it here. The lack of a consistent pattern in these correlations made it difficult to discern a predictive model of distribution of effort among fishing areas based upon the absolute CPUE values within an area only. These results suggest that, when studying the spatial allocation of effort among neighboring areas, local CPUE alone may not be insightful. Instead, it should be considered relative to the CPUE values in other spatial areas of the fishery, as shown in the previous section.

### Discussion

The theory of the ideal free distribution (IFD) has proven a useful way to understand distribution of fishing effort by generating hypothesis tests that follow from

a mechanistic model for the allocation of fishing effort across spatial areas. My analysis shows that the Hecate Strait trawl fishery meets the two assumptions of the IFD that I had data to test. Vessels move among areas (in a non-random way) and competition among vessels occurs such that they influence their respective catch rates. As well, the prediction of the IFD that I tested holds for the Hecate Strait trawl fishery: vessels tend to move among fishing areas so that catch rates (CPUE) are equalized among areas. Thus, the IFD theory should allow us to hypothesize how effort will respond to changing conditions in the future, and to aid in understanding patterns observed in historical data.

#### Prediction of IFD: Equalization of CPUE

The tendency for equality of CPUE among areas is consistent with Hilborn's (1985) statement: "The simplest starting assumption for studies of effort allocation would appear to be that vessels will move to equalize catch per boat . . . ". However, significant deviations from the IFD prediction do occur in the data, and they emphasize that a simple IFD is only a starting point for the examination of effort allocation. The next step is to understand the cause of these deviations.

In the complete data set and in the winter subset of the data, the slopes of the proportional regressions are significantly less than one. These deviations from the IFD prediction imply that there is an excess of proportional catch when the proportional effort is low, and a corresponding deficiency of proportional catch when the proportional effort is high. This is the type of deviation from the 1:1 line that would occur if interference competition among vessels increased disproportionately with increasing effort, causing the areas with high proportional effort to experience lower-than-average CPUE values. In addition to the relationship between effort and catch, other factors may influence profitability and cause the slopes to deviate from the IFD's prediction. Vessels may also be aggregating for reasons other than fishing, e.g. to

improve emergency response time in case of vessel damage or loss. In that case, the aggregating vessels would tolerate lower CPUE values than vessels that ignored risks and fished alone. Also, when information about newly available fishing locations is poor and the costs of acquiring it are high, those vessels aggregating on known fishing sites could experience lower CPUE values than solitary vessels encountering unexploited sites. Each of these cases would result in a slope less than one in the proportional regression. These factors may be reasonably associated with the winter months, when severe weather reduces the number of trips (and therefore reduces the available information), and increases the risk of vessel loss.

The deviations in the slope from the IFD prediction of 1.0 observed in the complete data set and the winter subset of the data could also be generated by a statistical artifact. Measurement error in the independent variable (effort) will reduce the magnitude of the observed slope in standard linear regression analysis (Draper and Smith 1981, Crittenden and Thomas 1989). Though I do not know the magnitude of this error, my slopes are close to the value hypothesized by the IFD, and vary around it. It thus seems likely that any effect of measurement error is minor relative to the other factors influencing my results.

Vessel movements associated with the gathering of information about concentrations of fish could also cause a deviation from a slope of 1 in the regression of proportional catch on proportional effort. Clark and Mangel (1983) proposed a dynamic optimization model that illustrated how fishing for information could influence the distribution of vessels. However, sampling by fishing is only one possible source of information on fish abundance. Recent landings, radio traffic and historical patterns provide less expensive means of assessment. Still, the first two of these other sources of information require that some effort is already being expended in an alternative area by other vessels. Exploratory individuals (termed "hunters" by Orbach 1977 and "stochasts" by Allen and McGlade 1986) may enter areas with low CPUE in order to

locate undiscovered fish sources. This searching behavior would result in low proportional effort values (exploring vessels) associated with disproportionately low catches (because of unsuccessful trial trawls with lower than average CPUE values). The resulting bias to the proportional catch-effort regression would be to cause the slope to be greater than one. This was observed in the summer data (Table 4), and may reflect more exploratory behavior in the fleet when weather conditions are relatively mild and total fleet activity is high. Also, in the regression of the complete data set (Fig. 2) the lowest proportional effort values have an excess of residuals falling below the fitted line and the IFD line. These low residuals could be the result of exploratory fishing in areas with little effort, even though the overall slope of the line is less than one.

Travel costs can greatly influence the profitability of a trip, especially when the landed catch is small. Generally, higher travel costs should be compensated for by a reduction in fishing effort and a correspondingly higher CPUE. This effect will be less pronounced when fish abundance (and therefore total profit) is high. However, the bias created in the regression of proportional catch on proportional effort by travel costs will depend upon the expenses and profitabilities of each area, and could increase, decrease or have no effect on the slope of the line. I was unable to identify a significant effect of travel costs in the Hecate Strait fishery, but this result is inconclusive because I used nonparameteric statistical tests for which power could not be determined.

### Competition Among Vessels

Previous studies of fleet dynamics have not explicitly tested for competition among vessels. However, competition is often assumed to be part of the causal mechanism linking the profitability of an area to the spatial allocation of effort (e.g., Hilborn and Ledbetter 1979). Competition exists in the Hecate Strait groundfish trawl fishery (Table 3). Also, the IFD prediction is most closely followed in the spring and

fall (Table 4) when competition appears strongest, (although only the competition test of the spring data is statistically significant, Table 3). The summer data (Table 3) fail to show significant competition, even though trips were most numerous at this time. In addition, the summer data (Table 4) show a significant deviation in the slope from the IFD prediction. Though lack of competition could permit aggregation of vessels in the most profitable area without a reduction in CPUE, there could be other possible explanations. But distinguishing among them is precluded by the lack of information on distribution of fishing vessels within the statistical areas. Also I do not know the statistical power of my competition tests, and therefore cannot confidently interpret the summer case where I failed to detect an effect.

The classic IFD is created by interference and not exploitation competition. The distinction between these two forms of competition must be made in order to determine the mechanism underlying the relationship between the distribution of catch and effort data. Unfortunately, I was unable to determine the form of competition in the Hecate Strait due to the variability of the data. It is probable that both forms of competition are present to some degree, but further research is required to quantify them.

### Movement of Vessels

The seasonal change in area-use strategies observed in Hecate Strait (Table 2) is consistent with the diverse nature of vessels in the fleet. The greater number of trips in the calmer months probably represents the entry of smaller, less mobile, vessels into the fishery. This is consistent with previous observations by Hilborn and Ledbetter (1979), who found that the salmon seine fleet could be divided into mobile and stationary components. The apparent equalization of CPUE among areas in the fall data (Table 4), when trips were numerous (Table 2), suggests that the flexibility of the mobile component of the fleet (moving between areas) is sufficient to maintain an IFD, even when a portion of the fleet remains within an area for the entire period.



### Local Response Hypothesis

I attribute the poor predictive ability of local CPUE (and its time lagged values) for indicating effort levels in an area (Table 5) to the presence of alternative fishing areas and the movement of vessels among these areas. Vessels that attempt to maximize their catch rate will be interested in the CPUE values of other fishing areas (i.e. the available choices), not just the absolute value of CPUE in one area. The lagged response of total fleet effort (all areas combined) to the average CPUE among the areas agrees with the results of previous studies (Hilborn and Ledbetter 1979; Millington 1984; Lapointe 1989) where increased CPUE attracted more effort in the overall fishery. However, even this relationship is not a strong one; its maximum rank correlation was 0.237 for a one-week lag. The weakness of this relationship could be due to alternative fishing or employment opportunities which are not considered in this analysis. For example, many of the vessels involved in the Hecate Strait bottom trawl fleet can also use midwater trawl gear to target on various rockfish species in areas just outside of the Strait. The opportunity costs created by an alternative fishery could have the same effect on total effort that the presence of alternative fishing areas has on the effort allocated within an area. This would result in a poor correlation between CPUE and total effort for the Hecate Strait trawl fishery, even if the fleet caught all of the target species of this study within the Strait.

### Implications for Stock Assessment and Management

The main implication of my results from the proportional regression analysis is that in situations where a fleet fishes among several discrete stocks or sub-stocks, the changes in CPUE values will not necessarily reflect trends in abundances within the stocks. In this case, a local decline in abundance in any stock would be tracked by changes in the proportion of fleet effort expended on that stock rather than the CPUE value.

As well, interference among fishing vessels will contribute to variability in the catchability coefficient ( $q$ ), which is usually considered constant (at least within an age class) in traditional stock assessment methods. The potential for  $q$  to vary with the abundance of fish is already known (Rothschild 1977, Peterman and Steer 1981, Peterman et al. 1985). Interactions among vessels could cause the true  $q$  value to decrease with increasing vessel density. As a result, the simple relationships that are assumed to exist between nominal fishing effort and fishing mortality in stock assessment may not hold. For example, if the number of vessels in a fishery has been increasing over time, increased interference could result in a temporal decline in  $q$ , and create overestimates of fishing mortality when estimates of  $q$  are based upon historical data. In an IFD, the effects of interference must be considered for each area in the fishery. Even if effort is increasing in the fishery as a whole, the influence of the other areas may cause local trends in effort to differ from the average.

My paper has looked at the multispecies catch of the Hecate Strait in terms of its total monetary value. However, it is common for species to have different population parameters in multispecies fisheries (Larkin 1977). Some species may be able to persist or even increase their abundance under a particular level of fishing pressure, while others may decline. If all species are caught indiscriminately by the fishing gear, the CPUE for each species may indicate trends in abundance (subject to my previous discussion). However, if fishermen can target effectively on certain species (by choosing area or depth to fish), an analogue to the IFD could develop for effort among the species. Fishing effort on the declining species would only occur when concentrations were high enough to be comparable to the other fishing alternatives.

The best remedial action for using catch and effort data in the presence of an IFD is to base stock assessment on independent research surveys rather than relying on data from the commercial fishery. The distribution of sampling effort to maximize information rather than profit and the timing of the work to avoid interference with

other vessels will avoid the potential hazards of an IFD. When this is not possible, then stock assessments should consider changes in the proportion of fleet effort among areas along with the changes in CPUE that have occurred. When the proportion of effort in an area declines while CPUE remains high, managers should be wary of a potential IFD and local stock reduction.

Determining whether interference and the IFD are present in a fishery is also important to understanding how the fishery may respond to future management regimes. For example, increasing either the size of the fleet or the time spent fishing per vessel will both increase fishing mortality. However, if interference is present among vessels, increasing the number of vessels would reduce the efficiency of fishing effort. Thus, if the effort (time fished) was raised by increasing the amount of time allowed for fishing by each vessel in the original fleet (e.g. by extending the fishing season), the increase in fishing mortality would exceed that of an expanded fleet expending the same amount of nominal fishing effort. Explicitly predicting patterns such as this would help managers to project the economic and biological effects of new regulations. The rationale for these predictions and the resulting decisions should be more easily communicated to the various interest groups involved with a fishery using the framework of the IFD.

Managers and researchers may not feel that my methodology provides enough information about the causes of vessel movement. If so, additional studies of both vessel and fish distributions will be required to determine if vessel movement is a source of bias in catch and effort data. However, before such potentially costly and difficult studies are undertaken, I would encourage the application of methods similar to mine to identify situations where more detailed research is most likely to provide useful results.

When the spatial scale of the catch and effort data encompasses an entire fishery, then a simple relationship between CPUE and effort may adequately model

effort allocation. But when the spatial scale of the data is small enough for the fleet to move among areas, the IFD should be considered as a model of vessel movement. When a fleet fishes distinct populations located within different sampling areas, the relative perspective of the IFD (each area's state relative to others' states) will be necessary in order to interpret CPUE values as an indicator of fish abundance.

## **Chapter 3            Dynamic discarding decisions: a study of high-grading in a trawl fishery using principles of optimal foraging theory**

### **Introduction**

Prey preference, or diet choice, is one of the founding topics of behavioral ecology (Emlen 1966, Pulliam 1974). The diet choice rule (Charnov 1976a) was initially developed to predict a calorically optimal diet based upon the abundance and value of alternative prey types. Since its conception, the diet choice rule, and the more general Marginal Value Theorem (Charnov 1976b) from which it led, have been successfully modified to account for a variety of conditions such as simultaneously encountered prey, lack of independence among prey encounters, and imperfect prey recognition (see Stephens and Krebs 1986 for a review). Recently, more complex mathematical methods, such as linear programming and dynamic programming, have been employed to predict diet choice in the presence of constraints such as gut capacity (Kaspari 1990), nutrient requirements (Belovsky 1978), and risk of starvation (Houston and McNamara 1985). All of these techniques (the marginal value theorem, its variants, linear programming, and dynamic programming) follow the general methodology of optimal foraging theory (Stephens and Krebs 1986); they all predict the diet of a forager by determining, based upon the available knowledge, the decisions that will provide the greatest benefit to the forager. In this paper I have used optimal foraging theory to determine which fish commercial fishermen should keep from their catch. I use the term fishermen to refer to both the men and women who are engaged in fishing as a livelihood.

In the past decade foraging theory has found many applications in qualitative and semi-quantitative studies of human foraging (see Smith 1983 and Foley 1985 for reviews). For example, diet choice theory has been used to make predictions about

foraging patterns under variable natural conditions in a number of modern hunter-gather societies, such as the Ache of Paraguay (Hawkes et al. 1982), the Siona-Secoya of Ecuador, and the Ye'Kwana and Yanomam of Venezuela (Hames and Vickers 1982), the !Kung San of the Kalahari desert (Sih and Milton 1985, Hawkes and O'Connell 1985), the Cuiva of Venezuela, and the Yora of Peru (Hill 1988). In these cases, diet choice theory has provided a useful focus for research, by providing clear hypotheses to test and directions for further study.

The methods of optimal foraging theory have also been applied to the behavior of fisherman. McCay (1981) found that observations of the number of species landed in a New Jersey fishery agreed with the qualitative predictions of diet breadth made by diet choice theory. Smith and McKelvey (1986) developed a game theoretic model predicting the proportion of specialist (fishing for a single species) and generalist (fishing for several species) strategies in the Oregon shrimp (*Pandalus jordaani*) fishery. Their predictions agreed with the observed trends in those proportions for 6 of the 9 years examined. Lane (1988) applied dynamic programming to predict trends in capital investment through time in the British Columbia salmon (*Oncorhynchus* spp.) troll fishery. Lane found a high correlation (86%) between his predictions and the total investment observed in the fishery.

The discarding of fish at sea is a problem of significant and increasing concern (Saila 1983). To the fishermen, the processing industry, and the marketing industry, these fish represent a loss of potential income, particularly when the mortality rate of discarded individuals is high. To the managers and scientists monitoring the fishery, discards are an uncounted component of the catch, which results in underestimates of fishing mortality and therefore poor estimates of population size and productivity (e.g. Pikitch 1991).

Fishermen cite several reasons for discarding fish at sea (Pikitch et al. 1988). Some fish are not retained because that species or size class has no market value.

Management regulations may cause discarding by prohibiting the landing of certain species or size classes. Also, regulations that limit the amount of a species or size class that can be landed may result in discarding, especially if the capture of other fish continues after the limit has been caught. At the end of a trip, fish may be discarded because there is no more room for them on the vessel. Finally, fishermen may discard potentially marketable fish in order to leave room for more valuable fish that they expect to catch before the end of the trip. It is difficult to determine which of these causes of discarding is dominant in a fishery without studying the actions of fishermen at sea. However, in the example of the Oregon trawl fishery, where such a study has been performed, management regulations were responsible for all of the discarding of yellowtail and widow rockfish (*Sebastes flavidus*, *Sebastes entomelas*) that was observed (Pikitch 1991, Pikitch et al. 1988). In general, discarding is more common when the amount of a species landed is limited by quotas, or when the abundance of that species increases (Pikitch 1987).

For my work, I have used three categories to describe discarding patterns: exclusion, capacity-discarding and high-grading. Exclusion is the discarding of particular species or sizes of fish because they are unmarketable or because there are regulations against retention of any of them. Capacity-discarding is the discarding of fish because there is no room for them on the vessel, due to either a full hold or a regulatory trip quota. High-grading is the discarding of potentially marketable fish so that there will be room for more valuable fish that are expected to be caught before the end of the trip. Exclusion and capacity-discarding are mainly the result of external pressures from the markets and the management agencies. However, even though it will be influenced by markets and regulations, high-grading is ultimately at the discretion of the skipper and crew of a fishing vessel; thus it must be examined from a behavioral perspective. My goal is to develop a model of high-grading behavior, treating fishing vessels as individual foragers. This model is based upon the same

principles as previous models of diet choice from foraging theory.

### **Fishing Vessels as Predators**

I treat entire fishing vessels as the predators of a commercial fishery, though I realize that the skipper and crew make the decisions that determine how to fish, where to fish, and what to keep during a trip. A mixed-species trawler captures its prey much like a larger version of the fish that they pursue. The trawl net, which is dragged behind the vessel at low speeds (under 5 knots) for times varying from minutes to over 2 hours during each haul, can be considered to be a large mouth (10's of meters wide) that engulfs fish as they attempt to swim away from it (Wardle 1986). Both the vessel's hold capacity (storage area below deck) and the management regulations limiting the amount of fish (in tonnes) that can be landed from a fishing trip are analogous to the gut of a foraging animal; they both limit the amount of captured prey that can be kept by a predator. Due to weather, benthic topography and sea conditions, fishing vessels (i.e., the skipper, crew and equipment) encounter the risk of injury and death while foraging, paralleling the risks of natural foragers (see Lima and Dill 1990 for a review of natural foraging under predation risk). When fishing, a groundfish trawl net typically brings up several different species and size classes of fish. The different types of fish in the net are analogous to a single prey item with body parts of differing values captured by a natural forager. Sorting and selecting the fish to keep occurs on the deck of the vessel, between the "mouth" (net) and the "gut" (hold). High-grading the catch is therefore analogous to partial prey consumption by other animal foragers (Cook and Cockrell 1978, Sih 1980, Lucas and Grafen 1985, Kaspari 1990).

However, from the perspective of diet choice theory, there is one important difference between a natural forager and a trawling fishing vessel. On a vessel, the crew can sort and discard fish from the previous haul while the net is being towed through the water again. This often eliminates the opportunity cost of handling time that



is central to much of diet choice theory (Charnov 1976a, Sih 1980, Lucas and Grafen 1985). Because handling time constraints may be minimized or eliminated when trawling, I chose to focus on absolute profit (the maximization of the total value of the landed catch at the end of a trip) rather than on the maximization of profitability (the average rate of profit throughout the trip) that is used in the marginal value theorem. I assumed that the gut capacity constraint (hold size or trip quota) was the motivation behind diet choice (high-grading) for my model of fishing vessels. This assumption is consistent with the reasons given by fishermen for discarding potentially marketable fish at sea (Pikitch et al. 1988).

Early work regarding gut limitation and partial consumption of prey by natural predators dealt with simple mechanistic models that lead to behavior similar to capacity-discarding (Holling 1966, Johnson et al. 1975). More recently Kaspari (1990) included gut capacity as a constraint in an optimality analysis performed using linear programming to study foraging decisions in grasshopper sparrows (*Ammodramus savanarrum*). Kaspari's model predicted partial consumption of prey before the gut capacity had been reached. However, his model still included prey handling (or preparation) as an optimization constraint and it did not generate the temporal dynamics of the decision process during a foraging bout. In order to include the temporal dynamics of high-grading within a fishing trip in my study (for comparison with field data), I chose a dynamic programming approach (Mangel and Clark 1988) to model the discarding decisions made by fishermen.

## Methods

There were four steps in my application of foraging theory to high-grading behavior. Initially, I identified a situation in a commercial fishery that would suggest the potential for high-grading, based upon direct observations and the principles of optimal foraging. Next, an optimality model of high-grading behavior in the fishery

that maximized the value of the landed catch was constructed using stochastic dynamic programming. Several parameter sets were used in the high-grading model in order to determine the sensitivity of the results to variation in the trip quota, availability of fish, and risk of early trip termination due to gear damage or injury. The results of the dynamic program were then used as the basis for "forward simulation" of fishing trips. These simulations generated the temporal trends in high-grading behavior, within a trip, that would be expected if the dynamic program was correct. Finally, the predicted patterns in high-grading behavior were compared to patterns observed during trips in the fishery under study.

#### The Oregon Sablefish Fishery

The Oregon trawl fishery for sablefish (*Anaplopoma fimbria*) for the years 1985 to 1987 provided data to apply foraging theory to the prediction of high-grading behavior. Trawlers generally capture a mixture of species, and the Oregon trawl fishery is no exception. However, sablefish form an important and readily identifiable component of the larger catch and high-grading is known to occur in this fishery from direct observation at sea (Pikitch et al. 1988). Foraging theory suggests that sablefish are likely to be subject to intraspecific high-grading because the value per kg of sablefish is greater for the larger size categories of fish: the largest sablefish were worth over twice as much per kg as the smallest during the observer study. This price structure allowed me to treat sablefish of different sizes as equivalent to the different prey types in classical diet choice models. The regulations governing the amount of sablefish that can be legally landed from a single trip are separate from those that govern the capture of other species in the fishery, so I could focus on the sablefish catch independently of the other species caught. The variations in these regulations through time provided contrasting situations, analogous to varying gut size, for testing hypotheses about the effect of total storage capacity on discarding patterns.

The data were originally collected from the Oregon trawl fishery as part of an observer study designed to estimate the extent of discarding under current management regimes (Pikitch et al. 1988, Pikitch 1991). Data were gathered by observers on vessels sailing from Newport, Astoria, and Coos Bay, Oregon. Vessel participation was voluntary, and the observers avoided influencing any of the decisions made by the skippers during the fishing trips. The weight of fish caught and discarded was estimated by the observers who sampled the hauls and extrapolated the contents of their sample to the entire haul, based upon the estimated total weight of the haul and the weight of the sample (Pikitch et al. 1988). The availability of fish in my model was defined by the contents of these hauls, and represents the abundance of fish as it was experienced by fishermen, which may not adequately reflect the abundance of fish in the ocean due to interactions between fishing effort and abundance (Rothschild 1977, Peterman and Steer 1981, Peterman et al. 1985). The decisions made by skippers (such as the choice of fishing strategies, the reasons for discarding, and the reason for ending a trip) were also recorded by the observers while at sea.

I limited my study to hauls that followed a deep-water trawling strategy because, in this fishery, sablefish are taken by hauls that target on species below 100 fathoms using mud-gear, roller gear, or combination mud-roller gear. Data were further limited because a detailed examination of the sablefish catch was only possible for a subset of the total number of deep-water hauls studied. Therefore the following sections indicate the number of trips or haul samples used to estimate parameters and test hypotheses.

### The Dynamic Program

Stochastic dynamic programming (Bellman 1957, Mangel and Clark 1988) is a numerical modeling technique used to determine optimal sets of decisions (strategies) that can vary through time until a finite time horizon is reached. The optimal decisions in a strategy are state-dependent, i.e. they depend on the current conditions, such as

fullness of the hold experienced by the decision-maker. The optimal strategies are also time-dependent, i.e. they can change as the decision-maker approaches the last time period. The collection of all optimal strategies for all time steps is the optimal policy. This policy is the solution of the dynamic program. The optimal policy is determined by maximizing the benefit to the decision-maker at the last time period. The main strength of this method is that it allows the effects of qualitatively different factors to be reduced to their effects on a single currency, at the time horizon. In my case, the availability and economic values of different fish, the trip quotas, and the risk to the fishing vessels can all be considered through their effect on the final value of landed catch. At any time throughout a fishing trip, the discarding decision that is most likely to maximize the value of the landed catch will vary with the amount of fish already stored in the hold (the state of the vessel) and the number of hauls remaining in the trip (the temporal dynamics).

The computational requirements for the solution of a stochastic dynamic program can be high, and are related to the definition of state variables and time periods. Both the time periods and the state variables must be approximated by discrete values if this numerical technique is used. The computational time required to find the solution of a dynamic program increases with increased number of time periods, state variables, or potential values for the state variables. Because of these limitations, I developed the most complex model that would execute in a reasonable time ( $< 1$  hour per run) on an IBM RS 6000/530. I modeled 14 time periods, representing 14 potential hauls of the trawl net, before the end of a trip. This maximum number of hauls was chosen to represent the number of hauls observed in the 1985-87 field data, which averaged of 7.5 deep-water strategy hauls per trip and ranged from 1 to 21 hauls. The model recognized three prey types, representing three size classes of sablefish with different economic values. The size classes were designated X, Y, and Z, corresponding respectively to the most valuable size class, the intermediately valued

size class, and the least valuable size class. The total capacity of the hold was discretized into thirty-one 226.8 kg (500 lbs.) units, so that the amount of fish that could be landed after a trip, without trip quotas, was between 0 kg and 6804 kg. The maximum capacity of the modeled vessels exceeded all of the trip quotas studied; thus it was these trip quotas that limited the amount of fish caught in my model.

Having defined the state-time space as above, the dynamic programming equation was written according to the form of Mangel and Clark (1988). This equation summarizes the value of being in a particular state at a specific time. This value depended here upon the trip quota and the value of each size class (both influencing the terminal value function), in addition to the availability of each size class at sea and the risk of premature trip termination. Following the notation of Mangel and Clark (1988), the dynamic programming equation defining the expected value of the amount of X, Y, and Z in the hold at the beginning of a particular haul (t) was:

$$1.1 \quad F(x,y,z,T,T) = \Phi(x,y,z)$$

$$1.2 \quad F(x,y,z,t,T) = \underset{d}{\text{Max}} (1-\Omega) \cdot \sum_{ijk} A_{ijk} \cdot F(x'_d, y'_d, z'_d, t+1, T) \\ + \Omega \cdot F(x,y,z,T,T)$$

where x, y, and z were the amount of X, Y, and Z in the hold,  $\Phi$  was the function that defined the value of any combination of values for the state variables at the end of a trip, T was the terminal time period (after the maximum of 14 hauls had occurred) when the trip was over ( $T=15$ ),  $\Omega$  was the probability of a premature trip termination during a haul, and A was a 5x5x5 matrix of probabilities representing the abundance of each of the size classes of fish found in the hauls. The indices (i, j, and k) of A represented the amount of X, Y and Z in a haul, quantified as discrete 226.8 kg (500

lbs.) categories. The values of the  $d$  index indicated the combination of size classes to be discarded if caught, and were defined as: 0 (X, Y, and Z), 1 (Y and Z), 2 (X and Z), 3 (X and Y), 4 (Z), 5 (Y), 6 (X), and 7 (none). The variables  $x'_d$ ,  $y'_d$  and  $z'_d$ , defined in detail below, represented the expected new values of  $x$ ,  $y$ , and  $z$  that would have remained after the decision  $d$  was made.

The range of catch values represented in  $A$  reflected the potential variability of weights per haul for each of the size classes. These values were based on observed weights in hauls employing a deep-water trawling strategy, which ranged from 0 kg to 790.2 kg. A 226.8 kg discretization of catches was chosen to match the discretization of the amount of fish in the hold described above. The 5 categories describing the amount of each size class in a haul were: 0 kg - 113.4 kg, 113.5 kg - 340.2 kg, 340.3 kg - 567.0 kg, 567.1 kg - 793.8 kg and, 793.9 kg - 1020.6 kg, corresponding to 0 kg, 226.8 kg, 453.6 kg, 680.4 kg and 907.2 kg. Thus, the matrix entry at  $A_{111}$  represented the probability of getting an empty haul, while the value at  $A_{555}$  was the probability of bringing in a haul containing 907.2 kg of each of the three size classes.

Equations 1.1 and 1.2 were used to determine the optimal discarding policy by working backwards from the final time period. In equation 1.1, the value of having  $x$ ,  $y$ , and  $z$  amounts of size classes X, Y, and Z during the final time period ( $t = T$ ) was simply a function ( $\Phi$ ) of  $x$ ,  $y$ , and  $z$ . At the penultimate time period ( $t = T - 1$ ), equation 1.2 states that the expected value of having  $x$ ,  $y$ , and  $z$  amounts of the three size classes was a function of the final composition of the landed catch ( $x'_d$ ,  $y'_d$ , and  $z'_d$ ) for all possible combinations of size classes in a haul ( $A$ ), discounted by the probability that only the fish currently in the hold would be landed because the penultimate haul could not be completed ( $\Omega$ ), and assuming that the discarding decision made for each of the possible haul compositions ( $d$ ) was the one that maximized the value of the landed catch in the final time period. Equation 1.2 modeled fishermen that based their discarding decisions ( $d$ ) on the expected contents of a haul rather than its

actual contents, i.e. they had poor knowledge of the exact contents of the haul currently being sorted. For a multi-species fishery like the Oregon trawl fishery in which the retained fish were being put in the hold as they were selected from the catch, it was reasonable to assume that the size distribution of one species in a haul would not be known until after all of the fish had been cleared from the deck. Once the expected values of all possible states had been determined for the penultimate time period, the process was repeated for  $t = T - 2$ , and then for  $t = T - 3$ , and so on until  $t = 0$ , the initial time period, was reached.

The state transition calculations for  $x'_d$ ,  $y'_d$ , and  $z'_d$  followed from the decision rules, the trip quota ( $Q$ ), and the amount of each size class that was available. For example, when size class  $X$  was to be kept (for decisions 1, 4, 5 or 7), then  $x'_d$  was calculated by adding the current amount of that size class in the haul to its current amount in the hold ( $x$ ). If the addition of the amount of the size class  $X$  in the haul would exceed the trip quota, then only the amount required to fill the quota was added to the hold. The remainder of the size class  $X$  in the haul represented capacity-discarding. When  $X$  was not being kept (for decisions 0, 2, 3, 6),  $x'_d$  was simply the amount of  $X$  already in the hold ( $x$ ). A similar procedure was followed to determine the values of  $y'_d$  and  $z'_d$ . After defining  $h = x + y + z$ , i.e. the amount of fish in the hold, and recalling that  $i$ ,  $j$ , and  $k$  refer to the amount of  $X$ ,  $Y$ , and  $Z$  brought up in a haul, the state transitions can be summarized by the following equations:

$$\begin{aligned}
 2.1 \quad x'_d &= x+i && | d \in (1,4,5,7); h+i \leq Q \\
 &= x+Q-h && | d \in (1,4,5,7); h+i > Q \\
 &= x && | d \in (0,2,3,6)
 \end{aligned}$$

$$\begin{aligned}
2.2 \quad y'_d &= y+j && | d \in (2,4,6,7); h+i+j \leq Q \\
&= y+Q-h-i && | d \in (2,4,6,7); h+i+j > Q \\
&= y && | d \in (0,1,3,5)
\end{aligned}$$

$$\begin{aligned}
2.3 \quad z'_d &= z+k && | d \in (3,5,6,7); h+i+j+k \leq Q \\
&= z+Q-h-i-j && | d \in (3,5,6,7); h+i+j+k > Q \\
&= z && | d \in (0,1,2,4)
\end{aligned}$$

Finally  $\Phi$ , the economic value of a simulated trip calculated at the last time period was defined as the value of the contents of the hold (the product of amount and value per kg of each size class) when those contents were less than the trip quota. However, the model conditions defined by  $\Phi$  excluded any landings that exceeded the trip quota. Thus,

$$\begin{aligned}
3 \quad \Phi(x,y,z) &= x \cdot V_X + y \cdot V_Y + z \cdot V_Z && | h \leq Q \\
&= 0 && | h > Q
\end{aligned}$$

where  $V_X$ ,  $V_Y$ , and  $V_Z$  were the prices of size classes X, Y, and Z per 226.8 kg.

### Estimation of the Parameters

Parameters for the availability of each size class, economic value of the size classes, trip quotas, and risk of premature trip termination were estimated from the data of the Oregon trawl fleet. The information required to estimate the parameters was not available in all of the haul records, so subsets of the data were used.

Records from 50 hauls that had the sablefish catch broken down by size class were used to simulate fish availability for the dynamic program. There were four



distinct market size classes in these data: extra-small ( $< 1.36$  kg), small (1.36 kg - 2.27 kg), medium (2.27 kg - 3.18 kg) and large ( $> 3.18$  kg). For my model, the medium and large size classes were combined into a single size class because both medium and large size classes were relatively rare in the catch, and reducing the number of size classes greatly reduced the time required to solve the dynamic program. Because larger fish were more valuable per kg, the field data were transformed into the 3 categories of my model by designating large and medium sized fish as X, small fish as Y, and extra-small fish as Z.

Preliminary analysis of the 50 hauls that had size class data showed that the amount of each size class in the catch was inversely related to the size of the fish and the availability of each size class in the hauls was correlated among the size classes. Therefore, I used the estimated availability of Z (the smallest and most numerous size class) to obtain the availability estimate for Y, and the estimates for both Z and Y to determine the availability estimate for X (the largest and rarest size class). The relationship among the size classes was not a simple linear one; the catch of one size class could be zero regardless of the amount of other size classes caught. However, when the zero points were excluded, linear regression of the logarithms of the catches between different size classes provided reasonable fits ( $P < 0.001$  for all regressions).

To deal with the cases of zero catches, the probabilities of catching none of size class X and Y in a haul were described by logit models. For Y, the amount of Z caught was the independent variable. Both the amount of Z and Y caught were used to estimate the probability of a zero catch of X. The parameters of these logit models were estimated using the non-linear estimation routine of the SYSTAT (Wilkinson 1989) computer package.

The relative availabilities of the three size classes were estimated by simulating 1000 hauls with the probability (logit) and regression equations estimated from the 50 real hauls. In this manner, hauls were generated that retained the variability and

correlation structure of the original data. The large number of simulated hauls, combined with the randomization of the residuals, generated a greater number of combinations of size classes than were present in the original 50 hauls, and allowed for the presence of possible combinations that may not have occurred in the original data due to the limited sample size. The distribution of the weights of each of the size classes in the 1000 simulated hauls were discretized into the categories of the A matrix. The probability, stored in the A matrix, of obtaining a haul with any particular combination of weights for the three size classes was defined as the proportion of times that the combination of weights occurred in the simulated hauls. In order to provide a range of values to examine the sensitivity of the dynamic program to the availability of fish, the A matrix was reconstructed by repeating the 1000 simulations with the original amounts of Z multiplied by a scale factor of 0.5 (low) or 2.0 (high).

The economic value of the three size classes was estimated from price data available for 23 trips landing sablefish from all size classes during the period of the field study. As mentioned previously, the value per kg of a fish was greater for the larger fish. A simple average was taken across all of the trips, with the prices for medium and large size classes pooled into a common category corresponding to the X size class in my dynamic program. Thus the high-valued size class (X) was \$1.41 per kg, the medium-valued size class (Y) was \$ 0.99 per kg and the low-valued size class (Z) was \$ 0.61 per kg.

The trip quotas used in the dynamic program were taken from those enforced by management agencies during the three years of the field study. They were: 2721.6 kg (6000 lbs.), 3628.7 kg (8000 lbs.), and 5443.1 kg (12,000 lbs.). There was also an additional 2268.0 kg (5000 lbs.) trip quota on the extra-small size class throughout the field study, but this was not considered in my model.

The risk of a premature trip termination was defined as the probability of an unforeseen ending occurring during a fishing trip due to injury, gear damage, or severe

weather conditions. Data for this estimate were taken from all of the available haul records from the field study. Risk was calculated for two-month periods by dividing the number of hauls during which a trip ended for unforeseen reasons by the total number of hauls during the two months. This level of aggregation of the data gave average risk values that peaked in December - January at 0.114 (13 of 114 hauls), and then declined exponentially to 0.007 in October - November (1 of 140 hauls). This trend was used as the basis for adopting 0.12, 0.08, 0.04 and 0 as a representative range of values for the probability of a trip ending prematurely during an haul.

Several solutions of the dynamic program were calculated to study the expected response of high-grading to changes in the values of the quota, availability, and risk. I examined the effects of modifying each of these parameters around the base condition, which was defined as: 1) a quota of 5443.1 kg, 2) unscaled availability, and 3) no risk.

### Simulated Fishing Trips

The results of the dynamic optimization are complex to interpret. The solution is a  $31 \times 31 \times 31 \times 14$  matrix containing the optimal decisions for all possible states (each combination of X, Y, and Z in the vessel hold) at all possible times. However, the behavior expected from optimal foragers (vessels) who use this decision matrix can be examined through the simulation of fishing trips where these optimal decisions are followed. This is known as the "forward simulation" of the dynamic programming solution. The parameters for the forward simulation were the same as those used for the dynamic program: availability, economic value, quota, and risk. In addition, the optimal decision matrix from the dynamic program was also provided as input.

The forward simulation modeled the progression of a fishing trip from start to finish, in contrast to the dynamic program, which performed its calculations by stepping backwards from the end of a trip. The simulated trips began with an empty hold. A random haul was generated, according to the probabilities defined by the A

matrix (see Appendix). The optimal decision for the availability, value, risk and quota values at the first time step was read from the appropriate location in the decision matrix and that decision was used to determine the disposition of the three categories of fish in the haul. The amount of each size class in the hold was then incremented as necessary and any discards were also recorded. The occurrence of a premature end to the trip was simulated if a random number, drawn from a uniform distribution between 0 and 1, was less than the current risk level. Otherwise, the time was incremented and the process repeated. The simulated trip ended after 14 hauls, after the quota was caught, or when a simulated accident occurred due to risk. 500 trips were generated for each set of parameters considered, and the resulting behavior was summarized as averages among these trips.

#### Comparison of the Model's Output to the Trawl Data

It was not possible to compare the detailed predictions of the forward simulation directly to the field data because the amount of each size class of sablefish discarded from each haul was not available. However, it was possible to compare the patterns of discarding observed in a portion of the field data to those that would be expected from the results of the forward simulation. This was not an absolute test of my model, but it was the best test possible with the data at hand. My goal in this section was to develop hypothesis tests (based on the results of the forward simulation, which are described in the following sections) that used the available data on discarding to determine if high-grading was occurring in the Oregon trawl fleet.

The dynamic program suggested that increases in the availability of fish could result in more high-grading because of the increased probability of filling the quota before the end of the trip. This hypothesis was tested by regressing the angular transformed proportion of the weight caught in a trip that was discarded on the availability of fish. Availability was estimated by the average weight of a haul within a

given trip. However, without trip quotas or hold constraints, the hypothesized relationship between the availability of fish and the amount of discarding observed should break down. The effect of quotas on discarding in the field data was tested by comparing the regressions of the transformed proportion discarded on availability between trips that had quotas and those that did not have quotas (excluding the 2268.0 kg limit on extra-small sablefish that was always in effect). The data from 48 trips were used for this analysis, 12 with trip quotas and 36 without them. However, a significant relationship between the proportion discarded and availability could also be caused by capacity-discarding because more trips that filled their quotas would result in more cases where some fish would be discarded from the last haul due to lack of space.

The feature that could distinguish between capacity-discarding and high-grading in the available data was the frequency of discarding through the progression of a trip. Capacity-discarding should occur only in the last haul of a trip if the quota has been caught. In contrast, the results of the dynamic program suggested that high-grading should generally become more common as a trip progresses. The temporal pattern of discarding within a trip was studied by correlating the transformed proportion of the discarded weight from a given haul with the standardized order of that haul in the trip. To exclude the influence of capacity-discarding from the analysis, I used only trips that (1) had more than 3 hauls employing the deep-water strategy, (2) landed sablefish in their catch, and (3) did not exceed their sablefish quotas; this limited the data to 42 hauls from 5 trips. The standardized order of a particular haul was calculated as the angular transformation of the proportion of the total number of hauls in the trip that the haul represented, for example, the second haul of a six-haul trip would be assigned the standardized value of  $\arcsin((2/6)^{1/2})$ . For each trip, I calculated the one-tailed P-value for the null hypothesis that standardized order of a haul and the proportion of the haul that was discarded were not positively correlated. The general validity of this hypothesis among all 5 trips was tested by pooling the results of all correlations in a

combined probability test (Sokal and Rohlf 1981, p. 779). The combined probability test was based on the fact that the sum of the logarithms of the P-values from  $n$  independent tests of the same hypothesis will have a Chi-squared distribution with  $2n$  degrees of freedom ( $df=10$  here).

## Results

### Simulated Fishing Trips

In the simulated trips, only the two least valuable size classes (the medium-valued size class, Y, and the low-valued size class, Z) were discarded (Tables 6 - 8). The low-valued size class (Z) always accounted for the majority of the discards. Theoretically, discarding some of the high-valued size class (X) could be optimal, if keeping all fish of that size in a haul would exceed the trip quota (capacity-discarding). However, none of the high-valued size class was discarded in any of the simulations performed. Thus, all of the discarding in the forward simulations was the result of high-grading behavior. The weight of fish discarded and the length of fishing trips varied greatly, even among simulated trips with the same parameters, because of the stochastic components of the catch and the risk of early trip termination. For example, among the 500 trips simulated for the base case (average availability of fish, 5443.1 kg-trip limit and no risk of premature trip termination) the duration of a trip ranged from 4 to 14 hauls, with a mean of 12.3 hauls. On average, 235.8 kg of the medium-valued size class was discarded, but the weight discarded ranged from 0 kg to 4.3 tonnes and had a median value of  $< 0.001$  kg; this indicates that for many trips there was little discarding of medium-valued fish class, but when it occurred large amounts of these fish were discarded. Highly skewed distributions in landed catches and discards were common in all simulations; these resulted from the skewed distribution of haul contents modeled by the A matrix.

Generally, the simulated high-grading increased throughout a trip (Fig. 3a - 3c), which is consistent with the reports of observers in the Oregon trawl study (pers. comm., Dan Erickson, Univ. of Washington). This temporal trend in my model resulted from the constraining nature of the trip quota and the stochastic nature of the catch. As a trip progressed, there was less uncertainty about the probability of filling the trip quota, and thus the decision to discard was more common toward the end of a trip. However, the relationship between the trip quota and the temporal trend in discarding was not a simple one.

Decreasing the trip quota increased the amount of high-grading observed and decreased the average length of a fishing trip (Table 6). The temporal pattern in discarding throughout a fishing trip differed between the two cases with low quotas (2721.6 kg and 3628.7 kg) and the case with the largest quota (5443.1 kg) (Fig. 3a). When the quota was largest, the mean proportion of actively fishing trips (i.e. excluding trips that ended by choice or due to risk) that were discarding fish increased through time from an initial value of zero. However, all simulated trips began by discarding some of their catch when quotas were low. For simulations with the 3628.7 kg quota, all of the simulated trips discarded fish during the first haul. During subsequent hauls, the level of discarding dropped suddenly, and then gradually increased through time, similar to the pattern observed for the largest quota. All of the trips that had the lowest quota (2721.6 kg) high-graded their catches during the first 5 hauls, after which the proportion of trips where discarding occurred declined, and levelled off at about 75 percent. The high incidence of discarding early in the trips with low quotas was caused by a high probability of quickly filling the trip quota with the most valuable size class when the quota was low. However, as the trip progressed, the stochastic nature of the catch resulted in some trips being unable to fill their quota. The potential for unfilled quotas resulted in the decline in discarding behavior observed after the fifth haul with a 2721.6 kg quota and drop in discarding that occurred between

Table 6. Sensitivity of discarding to the trip quota. Trip quotas used were taken from the regulations experienced by the Oregon trawl fleet from 1985 - 1987. X, Y, and Z are the high-valued, medium-valued and low-valued size classes of sablefish. Other model parameters are at their base levels (no risk, average availability of fish).

Tabulated values are the means across 500 simulations.

	Trip Quota (kg)		
	2721.6	3628.7	5443.1
X discarded (kg)	0.0	0.0	0.0
Y discarded (kg)	474.9	331.6	235.9
Z discarded (kg)	3247.3	2592.9	1437.4
% weight of X discarded	0.0	0.0	0.0
% weight of Y discarded	19.2	13.2	9.0
% weight of Z discarded	87.5	69.2	36.6
Average length of trip (hauls)	11.5	11.7	12.4



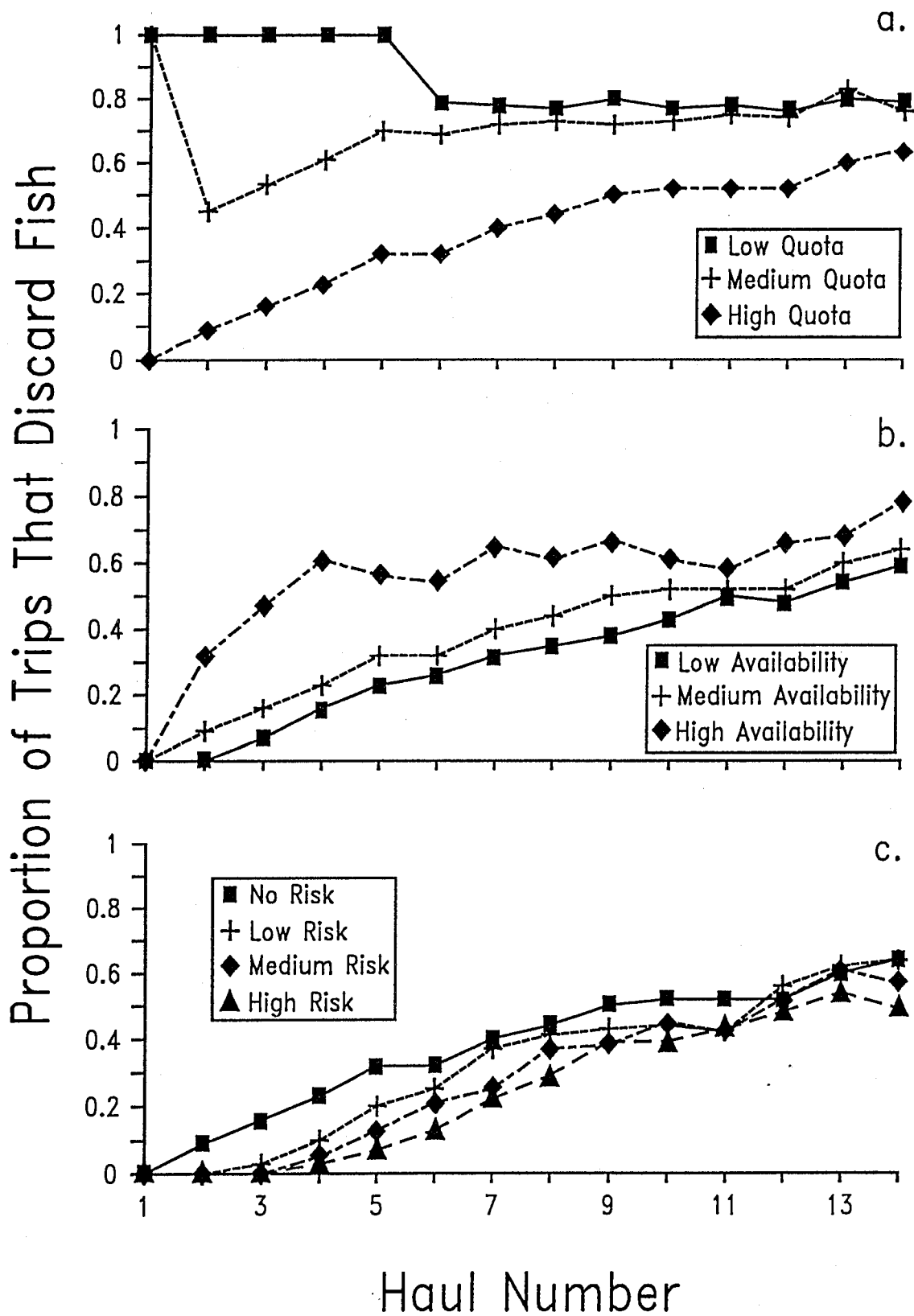
Table 7. Sensitivity of discarding to the availability of fish. Availability was initially defined by a matrix of probable catches (the A matrix) that accounted for correlations among the biomass of different size classes in the catch. Data from the observer study on the Oregon trawl fleet from 1985 - 1987 were used to construct this matrix. The fish availabilities were varied by multiplying the elements of the A matrix by three multipliers: 0.5 (Low), 1.0 (Medium) and High (2.0). X, Y and Z are defined as in Table 6. Other model parameters are at their base values (no risk, 5443.1 kg trip quota). Tabulated values are the means across 500 simulations.

	Fish Availability		
	Low	Medium	High
X discarded (kg)	0.0	0.0	0.0
Y discarded (kg)	284.4	235.9	220.0
Z discarded (kg)	923.5	1437.4	2600.4
% weight of X discarded	0.0	0.0	0.0
% weight of Y discarded	9.6	9.0	8.0
% weight of Z discarded	27.2	36.6	55.2
Average length of trip (hauls)	11.4	12.4	12.8

Table 8. Sensitivity of discarding to the risk of early trip termination. Risk is the probability that a trip will end for an unforeseen reason, i.e. crew injury or gear damage. The risk values used are representative of the range of risks encountered by the Oregon trawl fleet from 1985 - 1987. X, Y, and Z are defined as in Table 6. Other model parameters are at their base values (5443.1 kg trip quota, average availability of fish). Tabulated values are the means across 500 simulations.

	Risk Level			
	0.00	0.04	0.08	0.12
X discarded (kg)	0.0	0.0	0.0	0.0
Y discarded (kg)	235.9	126.1	59.4	40.4
Z discarded (kg)	1437.4	781.1	461.3	298.0
% weight of X discarded	0.0	0.0	0.0	0.0
% weight of Y discarded	9.0	6.3	3.7	3.0
% weight of Z discarded	36.6	25.7	18.9	14.9
Average length of trip (hauls)	12.4	9.2	7.1	5.6

Figure 3. The simulated sensitivity of high-grading behavior to (a) trip quota, (b) availability of fish, and (c) risk of premature trip termination. Lines show the mean proportion of cases that contained discarding behavior, based upon 500 simulated trips. However not all trips continued for 14 hauls; thus, the proportions for a particular haul were calculated from those trips that were actively fishing at that haul. In (a) the low, medium and high trip quotas were 2721.6 kg, 3628.7 kg, and 5443.1 kg. In (b) the low, medium, and high availabilities of fish represent simulations where the A matrix was constructed from the data after multiplying the estimated availability of the low-valued size class by .5, 1, and 2. In (c) the no, low, medium, and high risk levels correspond to a 0, 0.04, 0.08 and 0.12 probability of a trip ending, due to unexpected reasons, during a haul. The baseline values for the parameters in all three graphs were a trip quota of 5443.1 kg, medium availability of fish, and no risk of premature trip termination.



the first and second haul in trips with a 3628.7 kg quota. The stable 75% of trips that involved discarding in the later hauls for the lowest quotas represents an equilibrium between the active trips that are still well below the quota and those that are approaching it.

Variation in the availability of fish affected the discarding of medium-valued and low-valued fish differently (Table 7). Increasing overall availability decreased the amount and proportion of medium-valued fish discarded in a trip, but increased the amount and proportion of low-valued fish discarded. In addition, the average length of a trip increased with increasing availabilities. The greater length of trips was the result of fishing longer in order to fill the quota with both high and medium-valued fish. During these longer trips, more low-valued fish were discarded from the hauls so that the final landed catch would contain a greater proportion of more valuable fish. When the availability of fish was low, discarding the low-valued fish early in the trip could result in a final landed catch (after 14 hauls) that was below the quota and therefore less selective trips, which filled the trip quotas more rapidly, were favoured. Discarding increased with time for all three availability levels studied (Fig. 3b) but showed a distinct non-linear form for the highest availability level, reflecting the large amount of the low-valued fish, Z, that was discarded early in the trip to make room for the medium-valued fish, Y. High-grading was always more prevalent when availability was higher.

As might be expected intuitively, increasing the risk of early trip termination lowered the amount and proportion of both Y and Z that were discarded (Table 8). Also, the average trip length decreased with increased risk, as expected from the definition of risk in the model. Thus, in contrast to increasing the availability of fish, increasing risk shortened fishing trips and decreased the selectivity for certain size classes during those trips. With shorter trips, there was a greater chance of landing fewer fish than the trip quota, and therefore less discarding occurred. The temporal

pattern in the proportion of cases where discarding occurred (Fig. 3c) was approximately linear and increased for all risk levels studied. Also, throughout the trips, the amount of high-grading was generally greater for the lower levels of risk.

#### Comparison of the Model's Output to the Trawl Data

Analysis of the field data indicated the type of discarding that had occurred in the Oregon trawl fishery. When trip quotas were not in effect (Table 9a) there was no relationship between the proportion of the catch that was discarded during a trip and the availability of fish in the catch. However, when quotas were not in effect, a constant, non-zero, proportion of the catch was discarded. This is consistent with exclusion, where a component of the catch is never kept, and could result from the unmarketability of some component of the smallest size class. In the observer study (Pikitch et al. 1988) fishermen stated that over 30% of the sablefish that they discarded were too small to be accepted by the processing plants. When the same analysis was performed on those trips that occurred when trip quotas were in effect (Table 9b), there was a significant positive relationship between availability and the proportion of the fish discarded. This positive association could have been caused by a greater selectivity among size classes when the overall availability was high and when the amount of fish that could be landed was limited (high-grading), as I observed in my model. Alternatively, more capacity-discarding at the end of trips when availability was high could also generate this pattern. In any case, discarding behavior changed when trip quotas were imposed.

Examination of the temporal trends in discarding within trips distinguished between capacity-discarding and high-grading behavior. Discarding increased throughout the trip, as the forward simulation predicted, but for only 3 of the 5 trips that did not fill their quotas and for which data from all of the sablefish hauls were available (Table 10a). However, the combined trends of the 5 trips showed an overall

Table 9. The effect of availability and trip quota on the proportion of the catch discarded during a trip in the Oregon trawl fishery for sablefish. The following tables test the regression of the proportion of the catch discarded on fish availability. Fish availability was measured as the average weight (g) per haul for all of the hauls in a trip.

a. No trip quotas in effect while fishing, N = 36

Variable	Coefficient	S.E.	t	P
Constant	0.287	0.095	3.015	0.005
Availability	0.000	0.001	0.020	0.984

b. Trip quota in effect while fishing, N = 12

Variable	Coefficient	S.E.	t	P
Constant	0.039	0.098	0.395	0.702
Availability	0.118	0.001	2.587	0.027

Table 10. Combined correlation analysis of the temporal trend in the proportion of the catch discarded within a trip. Table 10a gives the results of the correlation between the catch discarded from the net (transformed weight) and the transformed order of the haul in the trip. Table 10b shows the results of the combined probability tests on the hypothesis that discarding increases throughout a trip. This test was only performed for those trips where there were data about the disposition of sablefish from each haul that caught them and the weight of sablefish landed at the end of the trip was less than the trip quota.

a.

Trip Number	Number of Hauls	r	P	Ln(P)
70	6	-0.774	0.938	-0.064
79	6	0.965	0.001	-6.908
80	5	0.935	0.010	-4.605
81	12	-0.537	0.964	-0.037
82	13	0.450	0.615	-0.486

b.

Number of trips	$-2 \sum \text{Ln}(P)$	D.F.	P
5	24.200	10	< 0.01



tendency for discarding to increase as a trip progressed (Table 10b). The presence of this relationship in cases where there was no apparent need for capacity-discarding suggests that high-grading behavior occurred in the sablefish fishery when trip quotas were in effect.

Though my model predicted that increased risk would decrease the amount of high-grading observed during a trip, I was unable to test this hypothesis with the available data. This was because the trip quotas that motivated high-grading in my model were only in effect during the high-risk months (August-December) in the field data; therefore, there was no subset of the data from the low-risk months for comparison.

## **Discussion**

The dynamic program and the simulation model of fishing trips that was based on it led to the following general prediction of discarding behavior: the extent of high-grading will increase when the probability of reaching the hold capacity or trip quota increases. The effects on high-grading behavior for all of the parameters studied arise directly from their effect on this probability. Thus, I expect that the amount of high-grading in a fishing fleet will increase when there is an increase in overall fish availability, or a decrease in the trip quota or risk of premature trip termination. However, my model suggests that increased availability of fish may not affect the discarding of all size classes in the same way. While discarding of the low-valued size class will increase with the increased availability of fish, the proportion of the medium-valued size class that is discarded will decrease if a greater profit can be expected from trips that retain them. Finally, my model predicts that discarding should become more common toward the end of a fishing trip; but when there is a high probability of the trip quota being filled exclusively by the most valuable size class, such as when quotas are low, this trend could be reversed.

As a behavioral model of prey choice, my dynamic program has generated patterns similar to those predicted by classical diet choice theory, but for different reasons. In classical diet choice theory the foraging rate is maximized by choosing the diet composition that yields the greatest average food value per unit of foraging time. Foraging time in such models includes the search, capture, preparation and consumption of each prey as exclusive events. Modifications to these models have considered factors such as decreasing prey value with handling (Sih 1980) and additional encounters that occur while handling prey (Lucas and Grafen 1985). However, in my situation, handling and prey preparation times play no role at all in determining prey choice. Furthermore, my model explicitly maximizes the profit at the end of a trip rather than the profitability of each haul within a trip. This is similar to other dynamic programming models of diet choice, which consider the value of foraging choices at the end of foraging bouts, rather than the rate of benefits obtained during the bouts (Houston and McNamara 1985, Beauchamp et al. 1992). In Houston and McNamara's theoretical study, surviving to the evening and minimizing the probability of starvation overnight was the goal of the foraging decisions made by small birds. In Beauchamp et al. (1992) common eiders (*Somateria mollissima*) chose the prey items and diving times that maximized their net gain of energy at the end of the foraging period.

The constraint that generates prey choice in my model is the vessel's capacity, limited by hold size or regulations, which I consider as analogous to gut capacity in other animal foragers. However, my work differs from earlier mechanistic models of gut limitation (Holling 1966, Johnson et al. 1975) in which foraging decisions were based on physiological causal relationships. Instead, the fishermen of my model try to make their decisions based upon the presumed outcomes of those decisions in the future. Other optimality models of the diet choice problem (Houston and McNamara 1985, Kaspari 1990, Beauchamp et al. 1992) have continued to consider handling time

as an important constraint in foraging decisions. While I do not deny this in the situations they considered, my model shows that temporally dynamic diet choice decisions can arise even without an opportunity cost due to the handling or preparation of prey items. The relative appropriateness of either viewpoint will depend upon the details of the system studied. In the case of other animal foragers, patterns similar to those that I have modeled for fishermen could be generated by a limited gut capacity combined with handling times that are small, handling times that are independent of the disposition of a captured prey item, or abundant prey types with differing nutritional values.

The analysis of my model was restricted to the main effects of trip quotas, availability of fish, and the risk of early trip termination. However, the general principle of maximizing the value of the landed catch governs how I expect these factors to interact. For example, if availability of fish increased when quotas were reduced, I would expect more discarding during fishing trips and also a possible change in the discarding practices, so that the proportion of discarding of the medium-valued size classes could drop. Alternatively, if quotas were increased when the availability of fish increased, their effects could cancel out and leave the amount of high-grading in the fishery unchanged.

High-grading does not vary uniformly across all values of the model's parameters. When the potential for catching more fish than can be kept is low due to long trips (with a greater number of hauls), high risk, high quotas, or low availability, variation in the value of the parameters that I have studied will have little effect on the predicted discarding behavior. In contrast, when the values of the model's parameters cause the probability of catching more fish than can be kept to become high, the predictions of the model will become very sensitive to changes in those parameters.

I did not examine the sensitivity of the model to the relative economic value of the various market classes. However, changes in these values could influence the

results of my dynamic program. Extreme changes in the relative values of size classes, that either make all fish equivalent in value or change the ranked order of values among the size classes, will invalidate the results of my model for the size classes studied. Changes in the economic values of size classes that decrease the differences among them will decrease the potential benefit of high-grading. However, as long as the value of the different size classes remains in the same rank order, there will still be benefits to the selection of size classes in the catch. Thus, I expect the predictions of my model to be robust to many changes in the market value of size classes.

My model assumed that fishermen could not estimate the abundance of the three size classes in a haul before it had been processed on board. In the case of experienced fishermen or when the contents of a haul were mostly sablefish, this assumption may not be true. However, the predicted behaviors from a model that assumed fishermen knew the contents of the current haul before making their discarding decisions would probably only differ slightly from my model. The amount of high-grading at the end of a trip would be less because late in a trip fishermen would not discard fish when there was actually room for them in the hold. In my simulation, fishermen may discard fish that could have been landed later in a trip if the amount of fish in a haul was below average. However, early in the trip the expected contents of future hauls would dominate the decisions of both formulations of the discarding model. In addition, the conclusions about the general effect of risk, trip quotas and the availability of fish would be the same in this alternative model as in my model: high-grading will be more common when the probability of landing the trip quota increases.

Data from the Oregon trawl fleet indicated that high-grading was occurring among sablefish of different size classes. Direct reports of high-grading by fishermen (Pikitch et al. 1988) show that it exists, but even without this evidence the haul data indicated the presence of high-grading behavior. When trip quotas were in effect, the increase in the proportion of fish discarded that followed an increase in the availability

of fish (Table 9b) could have been caused by high-grading, capacity-discarding or both forms of discarding. However, the overall increase in discarding as a trip progressed that occurred when the quota was not landed (Table 10b) was only consistent with high-grading behavior. As a result of limited data, my quantitative evidence for high-grading was based on only 5 trips; so few trips may not be representative of the behavior of the fleet. Additional data focusing on the sablefish portion of the Oregon trawl fishery will be required to develop stronger quantitative tests for high-grading.

The presence of discarding due to exclusion was indicated by the insensitivity of the proportion of the catch discarded to changes in the availability of fish when there was no trip quota for the total amount of sablefish landed (Table 9a). The regulation on the amount of the smallest sablefish that could be landed could not have easily generated a constant level of discarding. If this regulation were the cause, then large landings of sablefish should be associated with large weights of discarded fish. Instead, the constant proportion of weight discarded suggests that some sablefish, probably the smallest, were not acceptable by processors and therefore these fish were discarded as they were caught.

Models such as this can be useful both to those studying fisheries and those involved in making policy decisions about their management. Such models can help fisheries biologists to identify situations where landing statistics may underestimate fishing mortality due to high-grading at sea. Generally, cases where catch quotas are low or the availability of fish is high should be suspect. In both cases, if fish are high-graded by size, then today's profit will be paid for with fewer large fish in the future, because of the low survival rate of discarded fish (Saila 1983).

Regulations proposed by fisheries managers to extend fishing seasons or to conserve fish populations through the use of trip quotas or the limitation of fishing effort can be partially evaluated by considering the behavioral responses of fishermen that my model predicts. Even without quantitative details, it is clear that decreases in

trip quotas for particular species in a multispecies fishery will increase the incidence of high-grading, even while some trips are returning with less than a full hold or quota. Also, the potential influence of risk on discarding, shown by my model but untestable with the available data, suggests that reduced quotas are more likely to result in increased high-grading during the summer months than during the winter, when sea conditions make the risk of accidents at sea higher. Alternatively, effort regulations may provide a way to constrain fishing mortality without increasing the tendency for high-grading. Limiting the duration of a trip so that the vessel's capacity is not a constraining factor would circumvent the mechanism that I have proposed. These and other implications of effort and quota regulations for high-grading are examined in depth in the following chapter.

My model provides an example of how the principles of behavioral ecology can provide fruitful insights into current issues of resource use. It also provides the theoretical development of a situation where diet choice decisions arise without the effect of handling time. At the qualitative level, the model may help to identify new situations where diet choice is an important foraging decision. In order to apply this model quantitatively to human foragers (fishermen), detailed data will be required about the availability of each market class encountered, market prices, vessel characteristics in the fleet, and current discarding behavior of the vessels. With this information it will be possible to make predictions about how changes in biological (fish populations), economic (market prices), and regulatory conditions will affect the practice of high-grading at sea.

## Chapter 4      The implications of trip regulations on high-grading: a model of the behavior of fishermen

### Introduction

The incidental by-catch of unwanted marine life during fishing is one of the major political and biological issues of modern fisheries. Fish in the by-catch often consist of species and sizes that are unmarketable or have lower values than the target species. The less desirable components of the by-catch are usually disposed of at sea, and their capture is reported poorly, if at all. In some fisheries, such as shrimp (*Penaeus* spp.) trawling, discarded individuals may constitute the majority of the catch biomass (Slavin 1982). In other fisheries, a significant amount of the target species may be discarded because of their small size, such as 68% of the American plaice (*Hippoglossoides platessoides*) caught by trawling in the Gulf of St. Lawrence (Halliday et al. 1989) or 25% the North Atlantic cod (*Gadus morue*) caught by trawling (Kulka and Stevenson 1986). Furthermore, these figures may underestimate the actual amount of discarding occurring if fishermen are reluctant to discard in the presence of observers (Kulka and Stevenson 1986). However, discarding will be of little consequence if the discarded individuals are unaffected by the catch and discarding process. A knowledge of the survival of discarded fish is necessary to assess the impact of discarding on a fishery.

There are few direct studies on the ability of fish to survive discarding. It is generally believed that the mortality of discarded fish is high, and few discarded individuals survive to be caught again (Caddy 1982). Powles (1969) studied the survival of juvenile plaice on the decks of commercial fishing trawlers and concluded that over 95% of the discarded individuals were dead when they were returned to the water. Ricker (1976) cited discarding mortality estimates of between 1.9% and 86% for different Pacific salmon (*Oncorhynchus*) species and fishing methods (seine, gillnet,

troll), with most of the estimates falling between 30% and 50%. In Pacific halibut (*Hippoglossus stenolepis*), the mortality of discards varies among gears and regions. Estimates of the discarding mortality of halibut in the Bering Sea have ranged from 12% for individuals caught in groundfish pots to 100% in the trawl fisheries (Hoag 1975, IPHC 1991). These studies indicate that the potential mortality of discarded fish is high, especially in trawl fisheries. If so, discarding by fishermen would make fishery statistics unreliable sources for estimates of fishing mortality. This would clearly create difficulties in stock assessment procedures and evaluations of regulations.

The management of a multispecies fishery, where the selectivity of harvesting methods is limited, is a difficult problem. Managers must often make tradeoffs between the local welfare of certain species and the current economic value of the main fishery (May 1984, Pikitch 1988). The problem is made more complicated because simple regulations do not always have the desired effects. For example, regulations limiting the landing of certain fish may result in large unreported fishing mortalities of other fish due to discarding rather than the avoidance of the protected individuals by fishermen. This appears to be true in the Oregon trawl fishery, where fishermen claim that much of their discarding is due to regulations (Pikitch et al. 1988, Pikitch 1991).

Generally, agencies attempt to manage fisheries through regulation of the amount of fish that can be legally landed and the nominal fishing effort applied in a region. The amount of fish landed is often set to a single Total Allowable Catch (TAC) for a fishery within a year. This limit is then divided among several components of the fishery, often representing vessels with different gear types or nationalities (e.g. the Atlantic groundfish management plan 1991-1993, Fisheries and Oceans Canada 1990). The limitation of nominal fishing effort, often advocated on theoretical grounds, is difficult in practice. Generally, effort limitation has focused upon regulation of the size of the fleet (through licensing policy) combined with temporal and spatial fishing restrictions (Gulland 1974). Regulations are often designed to extend the fishery



temporally in order to stabilize the incomes of fishermen and to give all of them equal access to the resource. These limits may be reevaluated annually, quarterly, or at some other expedient time interval.

Recently, limits on individual fishing trips have become the focus of management regulations in both the Canadian and American Pacific coast trawl fleets (e.g. west coast groundfish management plan 1992, Fisheries and Oceans Canada 1991; also see Pikitch 1987, Pikitch et al. 1988). By regulating individual trips, a better control of the temporal allocation of effort and a more equitable division of the resource within the fleet could be obtained. However, my discussions with members of various sectors of the trawl fisheries suggest that these regulatory measures may increase the amount of fish discarded.

Discarding thus creates several problems. The marketable fish that are discarded due to regulations result in an immediate loss in revenue to the fishermen. If these losses become large enough, fishermen may lose confidence in the ability of managers to maintain a viable fishery, and become less cooperative when dealing with management agencies. Also, unreported fishing mortality can lead to poor estimates of future stock productivity. Discarded, dead fish will obviously not contribute directly to future catches and their potential reproductive contribution is also lost. When discards include the juveniles of the target species, the effects on future harvest can be severe (IPHC 1991). Even when the discarded fish are members of an unmarketable species, they may be important predators, prey or competitors for the commercial species (Garcia 1988). Ignoring the mortality of non-target species and size classes may thus make it difficult to understand changes in the marine community that result from fishing activities, and the subsequent effects on the commercial fishery.

Discarding can have many different causes. Regulations limiting the quantity or species composition of fish landed are commonly given by fishermen as the reasons for disposing of fish at sea. Marketability, and occasionally storage limitations (hold

capacity), can also result in discarding. Any combination of these factors may act together to create the pattern of catch disposition that is observed in a particular trip. I have chosen to categorize discarding according to the pattern (and bias) that it will create in the landings rather than the factors causing it.

The simplest form of discarding is **exclusion**. In this case, all individuals of a species or size class will be removed from the catch during the fishing trip. This may be due to the lack of a market or regulations preventing the landing of the discarded fish.

The second form of discarding is **capacity-discarding**. When the hold of a vessel is full, or when a regulatory landing limit is reached, all additional individuals that are caught will be discarded. On average, the species and size class composition of the discards will be the same as the catch. Capacity-discarding should only occur during the last haul of the trip, and its overall effect on fishing mortality will probably be slight. However, if the amount of one species landed is restricted by a regulation in a multispecies fishery, the discarding will continue as the vessel fishes for other legally landable species. The additional unreported fishing mortality that occurs for the regulated species during the latter part of such a trip could be quite large.

The final form of discarding is **high-grading**. In this case, fishermen selectively discard marketable fish in favour of more valuable ones throughout some or all of a fishing trip. The more valuable, retained fish may be in the same haul as the discards, or they may be expected to appear in future hauls before the trip is over. The ultimate goal of high-grading is to maximize the value of the total amount of fish that will be landed. High-grading may occur long before the hold is full, or before the trip landing limit is reached, though it should be more common toward the end of the trip when the amount of fish in storage is close to the maximum that can be landed. The species and size-class composition of discards resulting from high-grading behavior will be biased toward less valuable individuals, and could include members of the juvenile

age classes of the target species.

There is presently very little formal theory regarding discarding (see Hilborn 1985 for a discussion of the problem). This chapter focuses on high-grading because it represents a modification of fishing effort that results from decisions made by fishermen at sea. The amount of discarding caused by exclusion and capacity-discarding could be estimated from a knowledge of catch composition, vessel characteristics, market conditions and regulations. However, high-grading is the result of the more complex behavioral responses of fishermen to their natural and economic environments.

The question of when to high-grade is similar to the problem of optimal diet choice by natural predators, an active research topic in behavioral ecology (see Stephens and Krebs 1986 for a general review). In the optimal diet choice problem a predator is faced with several prey types, each with a different energetic or nutrient value and different abundances. The choice of which prey to keep in order to maximize energetic benefits depends on the dominant constraints faced by the forager (such as the handling time for a prey item or the gut capacity of the predator, Charnov 1976a, Kaspari 1990). Using these principles from behavioral ecology, I previously developed a model using dynamic programming (Bellman 1957, Mangel and Clark 1988), that considers the fishing vessel as a predator attempting to maximize the value of its landed catch while limited by the maximum length of the trip and the amount of fish that can be landed (chapter 3). The parameters of the model were estimated from field data on the contents of hauls and trip characteristics collected from the Oregon trawl fleet (Pikitch et al. 1988). The dynamic program predicted when (within a trip) high-grading would occur for the case of a single-species fishery with three distinct market classes of fish based on size. Comparison of the results of the model with additional data on catch disposition at sea showed a qualitative agreement between the predictions of high-grading in the model and the patterns of discarding observed in the field (chapter 3).

However, the effect of these decisions on the reliability of fishery statistics cannot be determined from the output of the dynamic program. That model's output is in the form of state-dependent predictions of the discarding decisions that will be made during fishing trips, given prescribed conditions. In order to study the potential interaction between high-grading and landing statistics I built a second model. This model simulated a fishery during one season, where the fleet was a group of fishing vessels whose behavior was generated by the state-dependent optimal decisions arising from my dynamic program. This second model is the subject of the current chapter.

The purpose of this study was to determine how the high-grading resulting from various within-trip regulations on effort and landings can affect landing statistics, the economic value of fishing trips to fishermen, and the allocation of effort among fishing trips. My study was based on the relatively novel approach noted above of simulating the behavior of fishermen using the principles of behavioral ecology in conjunction with field data. The resulting model begins to address the concerns raised by Hilborn (1985) by explicitly including the dynamics of fishing effort within a season in the evaluation of fishery regulations.

## Methods

### The Fishery

The data used to estimate the parameters of my model were taken from records of the Oregon trawl fishery. This was (and still is) a multispecies fishery employing a wide variety of trawling gears and strategies. I focused my work on a sub-catch of this fishery, the sablefish (*Anoplopoma fimbria*). These fish were marketed by size class, with larger size classes receiving higher prices per kg. There were 4 size classes for sablefish: extra-small ( $< 1.36$  kg), small (1.36 kg to 2.27 kg), medium (2.27 kg to 3.18 kg) and large ( $> 3.18$  kg). Because both the medium and large size classes were relatively rare in the catch, they were combined into a single large market class to

simplify my analysis. Thus there were three size classes for my model: the largest sized fish (X), the intermediate sized fish (Y), and the smallest sized fish (Z). In this fishery, regulatory limits on the amount of fish landed from a trip did not distinguish among the different size classes (above a minimum length of 56 cm, which was roughly equivalent to the extra-small size category). Thus, if a fisherman's catch exceeded the amount of fish that could be legally landed, it may have been more profitable to retain only the larger fish from the catch. Therefore, in this fishery high-grading was more likely to occur when regulatory limits on the tonnage of allowable landings were low or the abundance of larger size classes was high.

Data for this fishery came from an observer program conducted from 1985 to 1987 (Pikitch et al. 1988). The data collected by researchers in this program included information about samples from the hauls, the amount of discarding occurring, and the prices received for each size class. In addition, the program obtained details about the management regulations that limited the landing of sablefish during the study.

## The Model

### Overview

I used simulation modeling to evaluate the potential consequences of different management regulations on the amount of discarding expected due to high-grading, and the success of fishing trips for the fishermen. The model assumed that all fishing boats were equivalent and therefore it used individual fishing trips as the unit of fleet dynamics. These fishing trips were composed of a series of separate hauls. At the beginning of each haul, a decision was made about how much of each size class of fish would be discarded, if any. These discarding decisions were based on the amount of space remaining in the hold, the expected availability of each size class in the haul, the time left until the end of the trip, and other factors, as described in detail below.

Basing the discarding decisions in this simulation on the expected contents of a haul is equivalent to assuming that fishermen base their decisions on the average haul rather than the contents of the current haul. This situation could occur if fishermen have poor knowledge about the contents of a haul until after they have chosen which fish to retain from it. For a species like sablefish, which is dumped on deck as a component of a mixed-species catch, this is a reasonable assumption. Fishing trips were simulated until a predefined total allowable catch (TAC) for the season was landed. This TAC, as in most fisheries, referred to the catch that was landed and did not include discarded fish. The steps involved in simulating a season are summarized in Figure 4. I quantified the influence of different management regulations on discarding behavior and other measures of performance by repeating these seasonal simulations with the same TAC but using different regulations.

#### State Variables and Input Parameters

The present model used results from my previous dynamic programming model of fishermen's discarding decisions in a single trip (chapter 3) to determine the expected cumulative outcome of a series of trips. Consequently, the form of many of the variables and parameters in the present model was dictated by my previous model. In general, a stochastic dynamic program determines a set of optimal decisions for a system that depends upon the state of the system when a decision is being made and the time that the decision occurs (Mangel and Clark 1988). The optimization is based upon the probability of moving from one state to another in a unit time interval and the value of each of the possible states at the final time period. Thus, in the numerical form of this procedure that I employed, both the values of the states and the time intervals were defined in discrete units in order for the optimal set of decisions to be found.

In the both the simulation model and my previous dynamic program, the state of a vessel at a particular time during a trip was defined by the amount of each market class

of sablefish in the hold. Time within a trip was measured in terms of the number of completed hauls, progressing in unit increments from the beginning of the trip to its end. The hold of a vessel was discretized into 226.8 kg (500 lbs.) units, with a maximum capacity of 6803.8 kg. Thus in my model, the amount of any size class in the hold could only increase by some multiple of 226.8 kg. The actual hold capacities of the vessels involved in the Oregon fishery were larger than 6803.8 kg, but the regulated limits on landings used in the Oregon fishery, when in effect, were less than this maximum. Each simulated trip began with the first haul and an empty hold. In addition to the hold contents at each time, the amount of each size class discarded during a trip was also recorded to quantify the amount of discarding occurring.

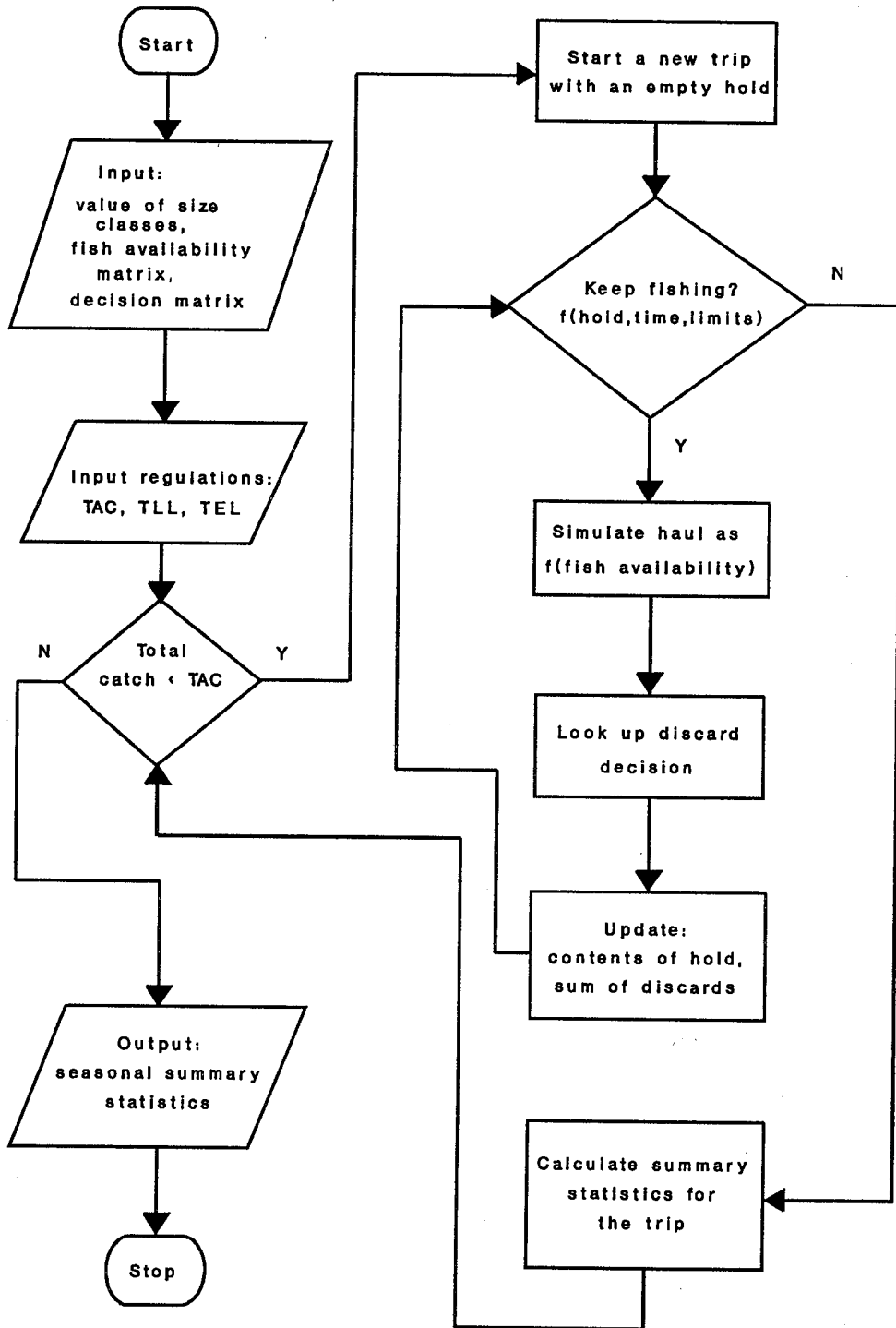
The simulation model's input parameters (Fig. 4) were the market value of each size class, the estimates of the amount of each size class that would be caught in a single haul (fish availability), the discarding decisions that would be made by the fishermen after a specific number of hauls when a particular amount of fish was in the hold, and the management regulations on the fishery, which I will discuss in a separate section below. Fish availability and the discarding decisions were both in the form of matrices whose values had been calculated during my previous work (chapter 3).

The market value of each size class was estimated from the prices paid for fish landed from 66 trips during the Oregon trawl study. The value of a size class per kg was defined as the average price paid for that size class across all of these trips. The prices for the two largest market classes in the data were averaged together to calculate the value that was assigned to the largest size class in my model.

The availability of fish was represented as the probability that a haul would contain discrete amounts of each of the three size classes of sablefish. Data from 50 hauls of the Oregon trawl fishery were used to estimate the availability of each of the size classes used in the simulated catch (see chapter 3 for details). I discretized the weights of hauls for each size class into 5 categories, based upon 226.8 kg increments,

Figure 4. A flow chart of the simulation of a fishing season, including simulation of discarding activity during each trip. TAC, TEL and TLL are abbreviations for the Total Allowable Catch, the Trip Effort Limit (in number of hauls) and Trip Landing Limit (in tonnes) respectively.





ranging from 0 kg to 907.2 kg. I then used the observed data to calculate the probability that a haul would contain a given categorical amount of the three market size classes. For example, the probability of a haul containing between 113.4 kg and 340.2 kg (represented in the model as the 226.8 kg category) of each of the three size classes was estimated as 0.043 from the field data. With 5 categories of haul weights for each of the 3 size classes of sablefish, there was a total of  $5 \times 5 \times 5 = 125$  possible combinations of haul contents to be considered. The probabilities of these combinations became the entries of a  $5 \times 5 \times 5$  matrix that reflected both the relative availability of the size classes of sablefish and the degree to which the abundances of the size classes were correlated. The sum of all of these probabilities, representing all possible contents of a haul, was one. This fish availability matrix, together with a uniform random number generator, was used to simulate compositions of hauls in my model so that they were similar to those experienced in the Oregon fishery.

The decision rules regarding which size classes to discard were derived from my earlier dynamic programming model. The dynamic program determined the discarding behavior of fishermen that would yield the highest expected gross profit when the value of the size classes, the fullness of hold, the maximum amount of time left in the trip, and the availability of fish were all known. The output of the dynamic program was a matrix of state-dependent decisions about which size classes to discard at a particular time with a given amount of fish in the hold. For example, if the hold contained the maximum amount of fish (the state) at any time during the trip, then the trip would end (the decision). If the hold contained no fish during the penultimate time step, then all size classes would be retained by the catch. With an intermediate amount of fish in the hold, the discarding of some of the size classes might occur, if that discarding could be expected to result in a higher value for the final landed catch.

### The Simulation of a Haul, a Trip, and a Season

The simulation of the events in a haul involving the capture, selection and storage of fish, was done in three steps (Fig. 4). First, the contents of a haul were randomly created using the fish availability matrix described above. The choice of which size classes in the catch to keep was taken directly from the output of the dynamic program (the decision matrix), according to the contents of the hold at that time and the time before the end of the trip (represented by the number of hauls which had already been made). Finally, the contents of the hold and the sum of the amount of each size class that was discarded were updated, based upon the discarding decision and the fish that were caught. As stated above, a trip was simply a series of hauls, beginning with an empty hold, and finishing when either the limit of fish that could be landed in a trip or the maximum duration of a trip, had been reached. The value of the landed catch at the end of the trip was calculated from the amount and value of each size class that was landed. The value of discarded fish was calculated in a similar manner. A fishing season was simulated as a series of consecutive trips, each beginning with no fish landed, and terminating when the total amount of fish landed equaled or exceeded the TAC. The actual number of trips in a season could vary, depending on the amount of fish that was landed per trip. The analysis of the model focused upon variables that were measured at the end of the trips and at the end of a season. In order to reduce the influence of rare stochastic events on the interpretation of the model, it was necessary to simulate 1000 seasons for each set of management options considered. The performance indicators that I used to evaluate the management options were averaged across these 1000 simulated seasons.

### The Performance Indicators

Variables produced as output from the model were those important to fishermen, managers or both. The goal was to calculate a set of indices that would allow decision

makers to compare the potential effects of varying regulations on different aspects of the fishery.

For example, both managers and fishermen are interested in the number of trips per season and the average length of a trip (measured here as the number of hauls). Regulations that lead to an increased number of trips will increase the importance of travel costs (such as fuel) to seasonal net profits, especially if the number of hauls per trip and the resulting catch per trip are reduced. However, regulations that increase the number of trips in a season and decrease the amount of effort per trip will tend to extend the fishing season. Developing regulations that maintain open fisheries throughout the year is often a goal of managers that is also favoured by fishermen.

Fishermen are also likely to be concerned with the economic value of a trip, the proportion of the allowable landing quota that is filled, and the market value of the fish that they have discarded. By definition, the gross value of the landed catch will have a direct influence on the trip's net profit. The proportion of the quota actually landed will influence the fishermen's opinion of the skill of the managers in choosing the regulations and potentially their future cooperation with regulatory agencies. For instance, if only a small portion of the allowable quota can be landed, fishermen will begin to doubt that managers adequately understand the system that they are controlling. Finally, the market value of discarded fish could cause concern and frustration in the fleet. Though fishermen are the ones who high-grade, they often perceive themselves as responding to market and regulatory conditions that have been forced upon them. In my experience, few fishermen are generally in favour of discarding, especially when the discarded fish have little chance of surviving to contribute to future catches. Regardless of the long term effects, it is important to know the immediate economic losses arising from discarding.

In addition to the conditions relevant to fishermen that result from regulations, managers are also concerned with the restriction of discarding-induced mortality and the

distribution of that mortality among age classes for the reasons discussed in the introduction. These aspects of the simulated fishery are represented by the total weight discarded per season, the proportion of weight initially caught that is discarded per season, and the weight of each size class discarded per season.

### The Management Regulations Examined

I examined the sensitivity of my model to a range of management conditions based upon those regulating the Oregon trawl fishery for sablefish between 1985 to 1987. During these years the trip landing limits (TLLs) on sablefish ranged from complete exclusion to no limit, and often included special provisions for size and the proportion of the total catch that was landed as sablefish. When TLLs were applied to sablefish of all size classes, they have ranged from 6000 lbs to 12000 lbs, or 2721.6 kg to 5443.1 kg in metric units. I used TLLs of 907.2 kg, 1814.4 kg, 2721.6 kg, 3628.7 kg, 4535.9 kg, 5443.1 kg, and 6350.3 kg, which I will refer to in this chapter as 0.9, 1.8, 2.7, 3.6, 4.5, 5.4, and 6.3 tonnes, respectively. I chose to represent the limitation of effort within a trip (TEL) by the number of hauls allowed, rather than a maximum trip duration because although time limits would probably be used in practice, my model was based upon data from individual hauls rather than time at sea. Due to the presence of other commercial species in the trawl fishery, more study would be required to equate the number of sablefish hauls to total fishing time. The range of TEL values used was based upon a maximum of 14 sablefish hauls per trip. In my sample of the Oregon trawl fleet, the fishing strategy that catches sablefish, when it occurred in a trip, was used for an average of 7.5 hauls (ranging between 1 and 21). The TELs explored here were 2, 4, 6, 8, 10, 12, and 14 hauls. A TAC of 14,000 tonnes was used to delimit a season of fishing in the simulation model. I simulated 1000 seasons for each of the 49 possible combinations of these TLLs and TELs in order to evaluate the sensitivity of high-grading behavior (and the associated indicators) to

management regulations.

### Sensitivity Analysis

This study was an analysis of the sensitivity of simulated high-grading behavior to a range of management conditions, but the computational requirements of my model were high and a full sensitivity analysis was not feasible. For instance, each run of the seasonal simulation model for all 49 different management conditions took up to a week to complete on an IBM RS6000/530 mainframe computer. This precluded extensive sensitivity analyses on the other parameters that were estimated from the historic data, such as fish availability and the economic value of size classes. However, two additional runs were performed using higher and lower fish availabilities; these were created by multiplying the expected amount of fish in a haul (estimated from the data) by a constant factor (2 or 0.5) and recalculating the fish availability matrix.

## Results and Discussion

### Effects of Regulations

The indicators varied with all of the combinations of trip effort limits (TELs) and trip landing limits (TLLs) used. For example, Figure 5 uses two superimposed plots to show that the number of trips per season decreased as the effort limit increased and that the number of trips was higher with a 1.8 tonne TLL than with a 4.5 tonne TLL. Because of the number of management conditions examined, the effects of both TEL and TLL on each indicator variable are best illustrated by an isopleth plot with TELs and TLLs on the axes and with contours through equal values of the indicator. For example, the number of trips per season is shown as a function of trip effort limits and the full range of trip landing limits in Figure 6, where the contours connect equal numbers of trips per season. Figure 5 can be viewed as two vertical cross-sections through Figure 6, one at TLL = 1.8 tonnes, and the second at TLL = 4.5 tonnes.

Figure 5. The number of trips required to achieve the TAC of a season for two different trip landing limits (TLLs) and several trip effort limits (TEs).

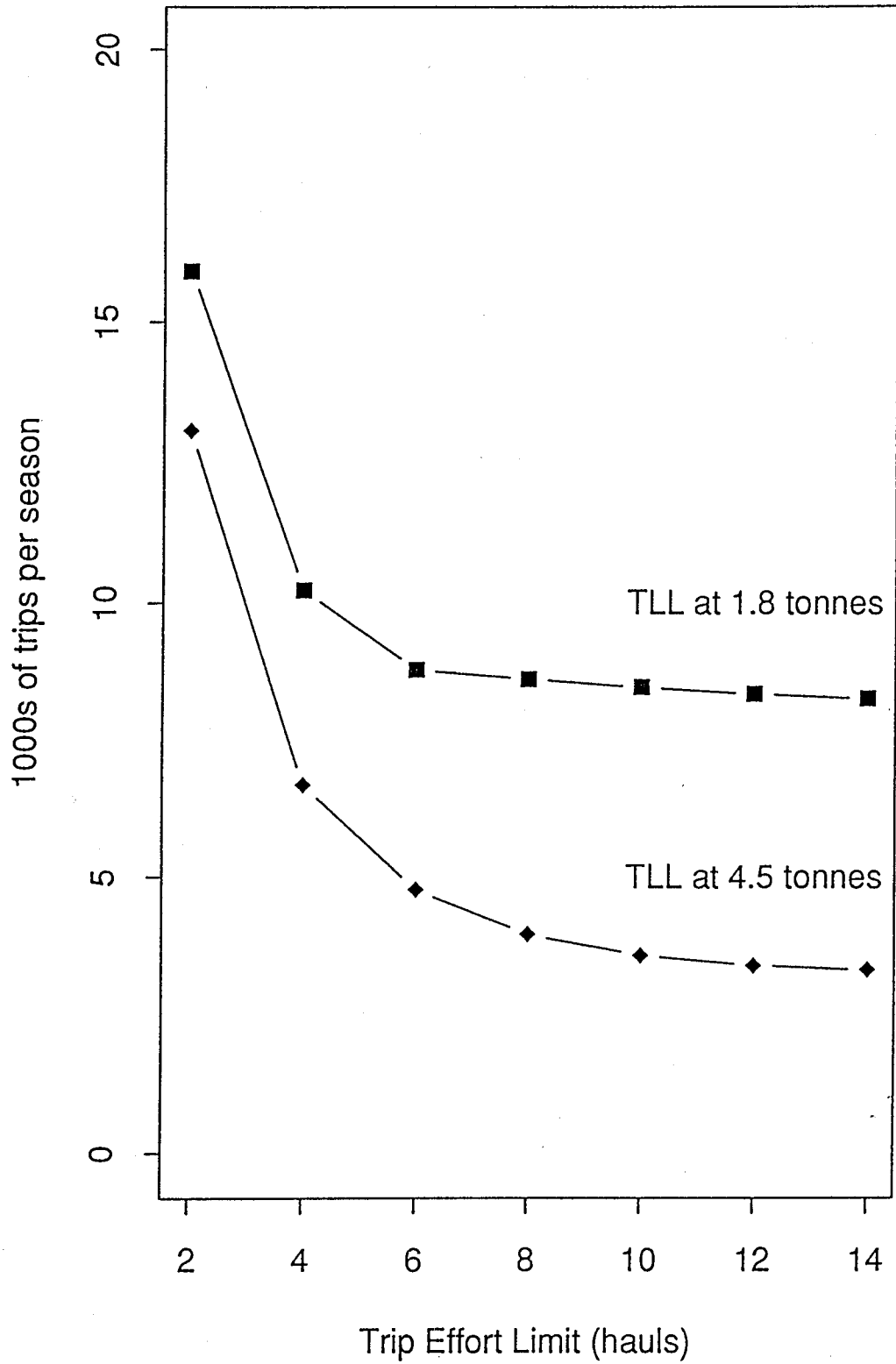
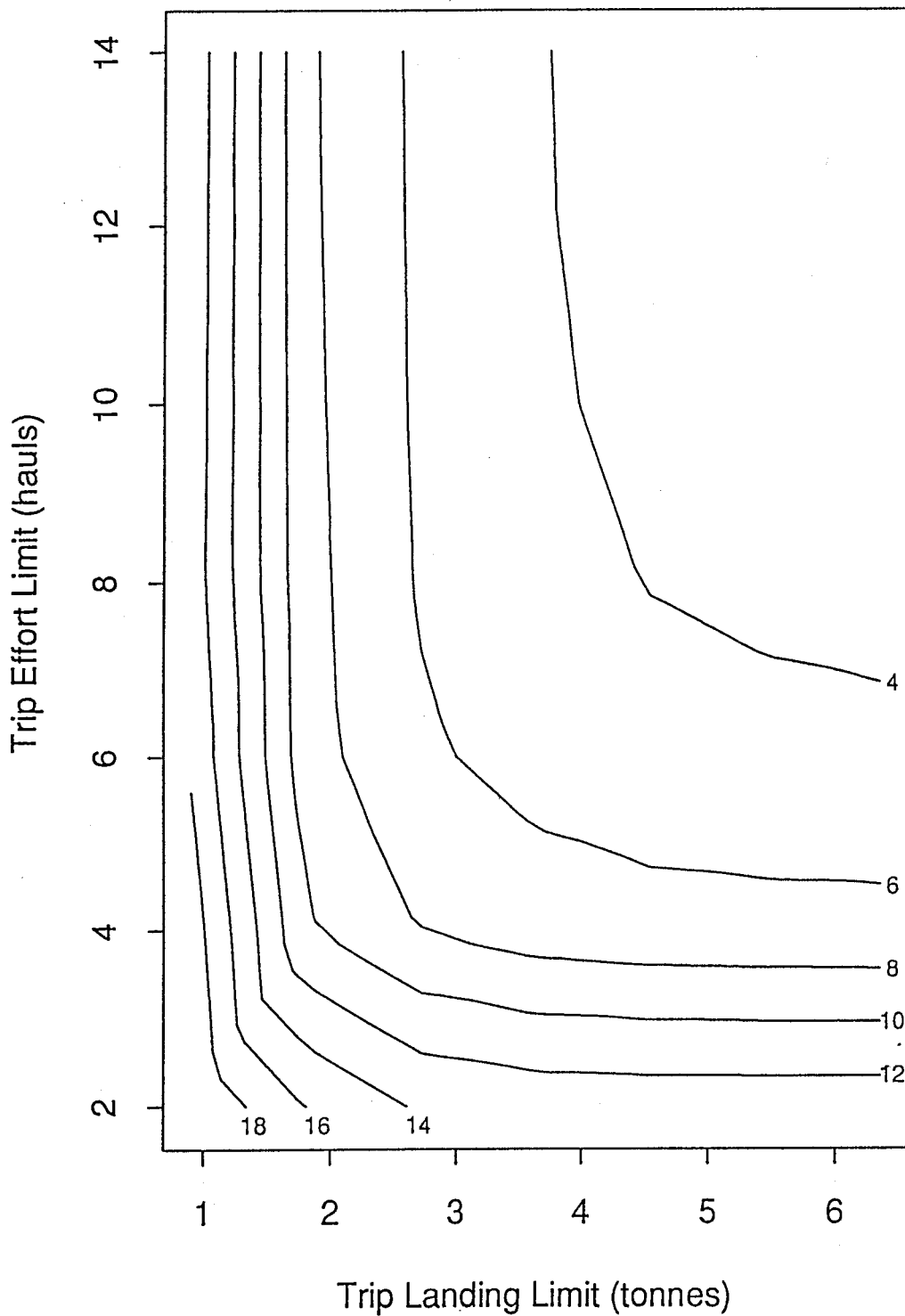




Figure 6. The number of trips required to achieve the TAC of a season for a range of trip landing limits (TLLs) and trip effort limits (TELs). Each contour represents a set of conditions that result in the same number of trips in a season.

# 1000's Of Trips Per Season



The number of trips per season was greatest at low TELs and TLLs (the lower left corner of the graph), which was expected with a fixed TAC; when there was less opportunity to catch fish in a trip, due to a low trip landing limit or a low effort limit, more trips were required to land the same amount of fish. In the upper right corner of the graph, there is a basin, which indicates that the number of trips per season was low and relatively insensitive to variation in TELs and TLLs when both regulatory limits were high. This insensitivity suggests that when both regulatory limits had high values, they were less of a constraint than fish availability (the only other factor limiting catch in my model) on the amount of fish landed per trip and therefore the number of trips required to land the TAC. In the upper left corner of Figure 6, representing high TELs and low TLLs, the number of trips per season was highly sensitive to changes in the TLL, but not to changes in the TEL. This is indicated by the nearly vertical orientation of the contours for cases where the TLL was less than 2.7 tonnes. The sensitivity of the number of trips to changes in the TLL suggests that this value was significantly limiting the amount of fish that could be landed from a trip in this region of the graph. The TEL did not obviously influence the number of trips in a season until it dropped below 8 to 10 hauls per trip. For cases where the TEL was at its lowest and the TLL was high, the contours of equal numbers of trips per season were nearly horizontal (lower right of Fig. 6), indicating that in those cases the TEL had become the limiting factor for trip landings.

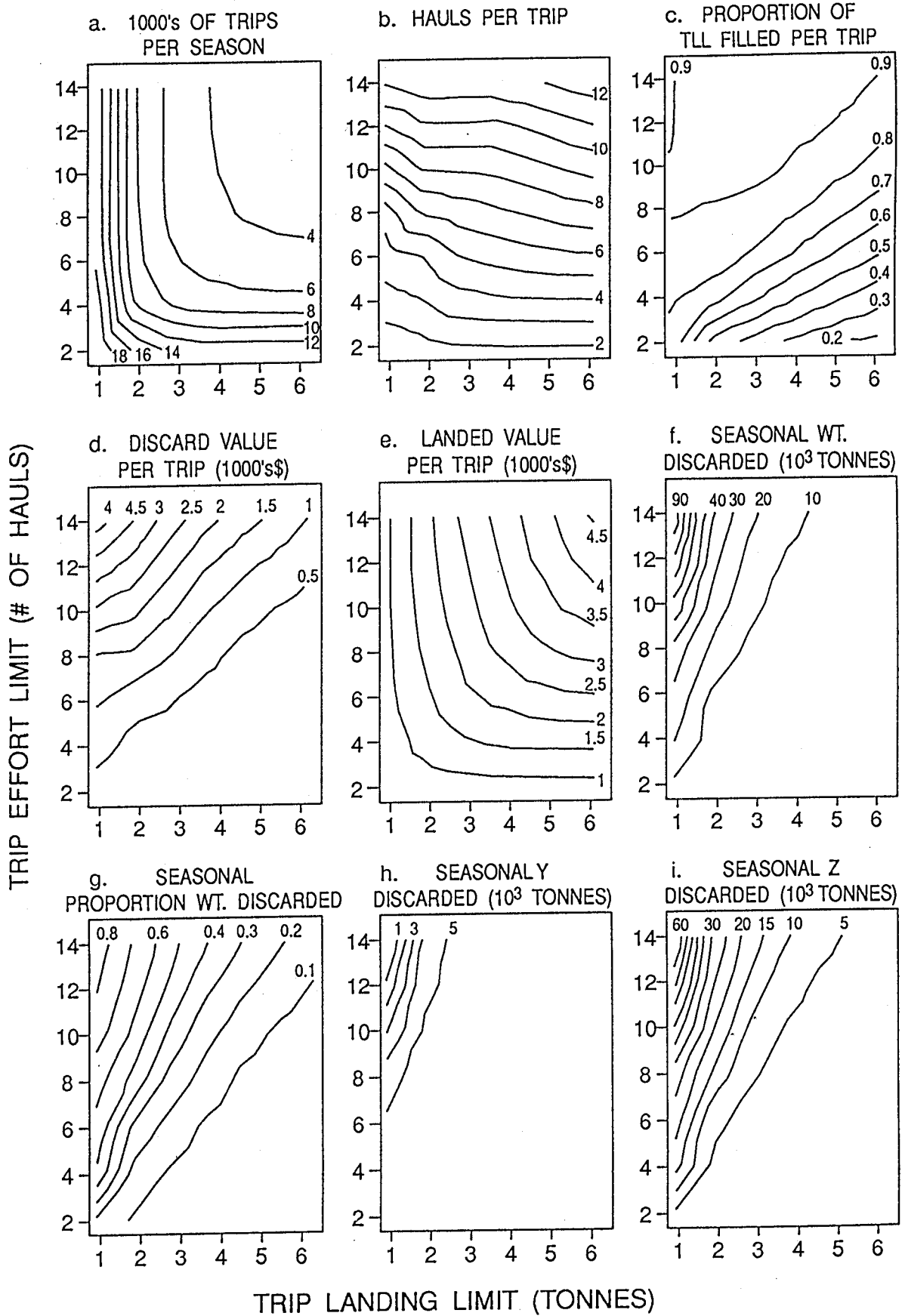
To summarize Figure 6 (also Fig. 7a), when the TLL was greater than 4 tonnes and the TEL was greater than 8 hauls per trip, there was little regulatory effect on the number of trips required to catch the TAC in a season. However, below these values the number of trips required increased. The number of trips per season was most sensitive to changes in the more severe of the two regulations. When landings and effort were both strongly limited, the number of trips was equally sensitive to changes in either regulation.

The contours of equal value on the isopleth graphs for the other eight indicators (Fig. 7) can be interpreted similarly to show the sensitivity of these indicators to the different combinations of effort and landing regulations that I examined.

The number of hauls per trip (Fig. 7b) increased only slightly with increasing TLL. In contrast, the number of hauls per trip was very sensitive to TEL. For a given TLL, the average number of hauls per trip increased with increasing TEL, but was always less than the TEL. The difference between the TEL and the number of hauls was due to the stochastic nature of the catch, which resulted in some simulated vessels filling their quotas before their TEL was reached. These trends indicate that trips tended to go on as long as possible, high-grading to avoid exceeding the TLL and finally terminating when the TLL was reached. The shape of the contours, turning upward at the left of the graph, indicate that the lowest TLL had an unusually large number of hauls per trip for all effort limits. The longer trips resulted from more severe high-grading for the lowest TLL, involving a greater frequency of discarding behavior during a trip and the discarding of more size classes, as shown indirectly by Figure 7g. Intense high-grading would be more likely to be profitable when the limits on landings were low, so that there would be a greater probability of filling the TLL with the most valuable fish.

For a given TEL, the proportion of the TLL filled within a trip generally decreased as the TLL increased (Fig. 7c) because for a given availability of fish, there was a lower probability of reaching a landing limit as the limit increased. Conversely, for a single TLL, increases in the TELs resulted in a greater proportion of the TLL being filled, due to the increased opportunity to fill the landing limit through more hauls. However, there is a plateau in the upper left region of Figure 7c, which represents cases with high TELs and low TLLs. The height of this plateau, where less than all of the TLL was filled, was the result of high-grading behavior. Without high-grading I would have expected the proportion of the TLL filled to continue up from a

Figure 7. The variation in the nine performance indicators under a variety of management options. TLL and TEL are defined as before. The response of each indicator to the different regulations is shown using isopleth diagrams.



TRIP LANDING LIMIT (TONNES)

plateau at 1.0, because with low TLLs and high TELs there was ample opportunity to fill the landing limit. However, discarding some of the catch in favour of more valuable fish in future hauls resulted in some trips that did not fill their TLL. The stochastic nature of the availability of fish in my model contributed to this shortfall in the landings by creating situations where catches of higher quality fish did not occur before the end of the trip. This does not mean that high-grading was a poor decision (the decisions in the model are optimal by definition), but instead it means that on average it was more profitable to leave room for a possible catch of high quality fish than to always land the full TLL. High-grading also caused combination of the lowest TLL (0.9 tonnes) and the highest TEL (12 and 14 hauls) values to fill less than 0.90 of the landing limit and fall slightly below the plateau values. In these cases, where the opportunity to catch more high quality fish was greatest, the strongest high-grading occurred, as suggested previously for the upper left corner of Figure 7b.

The economic value of the fish discarded during a trip (Fig. 7d) increased when TEL was increased, reflecting the greater amount of high-grading that occurred when there was more opportunity to catch fish. In contrast, when the TLL was increased, the total value of the discarded fish decreased because of the decrease in high-grading that accompanied less restrictive TLLs. The greatest total value of discarded fish, because of the greatest amount of high-grading, occurred for the 0.9 tonne limit on landings and the 14 hauls limit on effort.

Not surprisingly, the value of a trip to a fisherman (Fig. 7e) is greatest when the TLL and the TEL are greatest; both regulatory actions appear equally effective at causing a change in that value. However when either TEL or TLL were low, the value of a trip was unresponsive to changes in the other regulatory measure. Like Figure 7a, Figure 7e suggests that at low values of the regulatory measure, either of the regulatory actions could limit the maximum economic value of a trip. Unlike Figure 7a, the value of a trip could still be increased by increasing either of the limits when both regulatory

measures had high values. In short, both regulations limited the gross profits from a trip, and the trip value was maximized when regulatory actions were minimal.

The trends in the value of the fish landed from a trip and the value of the fish discarded provided an insight into an interesting contrast that could occur in a real fishery. Comparing Figures 7d and 7e shows that the combinations of regulations that favoured high-grading often resulted in the value of fish discarded exceeding the value of fish landed (e.g. for a TEL of 14 and a TLL of 1, the value of discarded fish exceeded \$4,000 while the value of the fish landed was less than \$1,000). Even though the value of fish being landed from a trip was maximized by the discarding decisions, it is unlikely that either fishermen or managers would be content with a situation that was so obviously wasteful.

All indices of discarding over the entire season (Fig. 7f-i) shared the same pattern as the economic value of the discards during a trip (Fig. 7d); they increased when the TEL was increased and they decreased when the TLL was increased. However, unlike Figure 7d, the rate of change in the weight of fish discarded during a season (Fig. 7f,h,i), indicated by the distance between the contours, was not constant. This rate accelerated towards the upper left corner of the graphs, revealing that the sensitivity of the weight discarded to changes in regulations increased when TEL was high and TLL was low. The increased sensitivity of discarding to regulations would be expected with the onset of high-grading behavior which occurred during conditions that allowed a vessel to catch more fish than it could keep (i.e., low TLLs and moderate to high TELs). The total weight of fish discarded from all size classes varied greatly with the combination of regulations in effect, ranging from less than 10,000 tonnes to over 90,000 tonnes. The majority of the discards were from the least valuable size class, Z (Fig. 7i), because high-grading discriminates against the less valuable size classes in favour of retaining the more valuable fish. Within this size class, the seasonal discards ranged from less than 5,000 tonnes to over 60,000 tonnes (Fig. 7i). Some of the



second most valuable size class (Y) was discarded under conditions favouring high-grading (Fig. 7h), but the most valuable size class was never discarded. The total weight of fish discarded in any size class depended on two factors. First, the amount of more valuable fish available determined when the discarding of a size class would occur (chapter 3), and secondly the amount of the size class in the catch determined to actual amount discarded. Thus, the quantities of discards in Figures 7 f, h and i were the result of the particular set of availabilities for the size classes used in this model. However, high-grading will always be a more severe problem for the least valuable fish, discriminating against them first regardless of the relative abundances of alternative species or size classes.

The range in the proportion of the initial catch discarded per season (by weight) varied over the range of regulations studied from less than 0.1 to over 0.8 (Fig. 7g), and corresponds to the patterns in high-grading behavior that were discussed previously. The potential for TELs and TLLs to result in discarding over 80% of the total weight of fish caught in a season emphasizes the potential sensitivity of high-grading behavior to trip regulations implemented by management agencies.

Varying the total availability of fish by a constant factor did not change the general results observed in Figure 7. There were some quantitative differences among the runs. For example, when the availability of fish was halved, the maximum proportion of the catch that was discarded was between 0.7 and 0.8, rather than over 0.8 as in the base case and the case where the availability of fish was doubled. Overall, the differences among the runs were minor and do not warrant further discussion.

In summation, Figure 7 quantifies, to my knowledge for the first time, the combined effects of regulatory limits on trip effort and landings per trip on numerous relevant indicators. These results clearly illustrate that the manner in which regulations are imposed can strongly influence the extent of discarding arising specifically from high-grading behavior. The differences among the effects of regulations occur even

though the availability of fish and total allowable catch were constant. This modeling approach, based on the available data and incorporating the behavioral responses of fishermen, provides a useful method for evaluating the potential consequences of proposed regulatory actions.

### Management Implications

I have not defined the relative importance of the indicators in Figure 7; this would need to be done in a final analysis of any proposed regulations. Many different response variables can be considered in a multiattribute analysis of decisions (Keeney and Raiffa 1976). A formal presentation of this technique is beyond the scope of the present work, but it essentially involves weighting each indicator variable and then combining them through an objective function into a single utility value which is to be maximized.

In practice, managers may want to weight various indicators based upon regional social needs or the expected long-term biological consequences of the regulations (Smith 1980, Wooster 1988, Fisheries and Oceans Canada 1990). For example, managers may want to minimize discarding (Fig. 7g), while attempting to keep both the economic value of a trip (Fig. 7e) and the proportion of the landing limits that are filled (Fig. 7c) high. The model indicates that these management goals would be met by large trip landing limits and trip effort limits, corresponding to the upper right region of the graphs in Figure 7. This region has the most desirable values, according to the stated objectives, for each of the three indicators under consideration.

Additionally, managers may want to include another factor in their objectives: to spread fishing effort more evenly throughout a season by increasing the number of trips required to land the TAC (Fig. 7a). This is a common reason for the implementation of trip landing limits in fisheries (e.g. Pikitch 1987, Fisheries and Oceans Canada 1990). My model indicates that this could be achieved either by decreasing the TLLs

or the TELs from the levels discussed above, but both approaches will result in less desirable values for some of the indicators. The reduction of either limit will cause similar reductions in trip revenues (Fig. 7e), the reduction of the TLL alone will result in increased discarding (Fig. 7g), and the reduction of TEL alone will result in a smaller proportion of the TLL being filled in a trip (Fig. 7c). If both TEL and TLL were both reduced, there would be little effect on either the proportion of the catch that was discarded (Fig. 7g) or the proportion of the TLL filled during a typical trip (Fig. 7c). The best combination of TEL and TLL regulations for the fishery will depend on the weights that the managers assign to each of these indicator variables in their objective function.

My analysis in its present form does not provide valid recommendations for sablefish management in the Oregon trawl fleet. It is only a general analysis of the discarding process based on subset of data from that fleet. To justify specific application to the Oregon situation, further refinements of the model in many areas would be required. For instance, a definition of effort in the model which provided a closer approximation to actual time at sea would be necessary. This will be especially difficult in a multispecies fishery, such as this one, where entire trips may catch the regulated species as a bycatch while pursuing other target species.

#### Factors Omitted

There were many factors that I could not consider in this work due to lack of data or the amount of time that would be required to rerun both the dynamic program and the simulation model. The market values for the size classes, the relative availabilities of the size classes, and the influence of the costs of fishing on high-grading are all examples of factors that would require a complete reanalysis to study the effects of changing their values. However, there are reasons to believe that the results of my model are at least qualitatively robust to many of these factors.

For instance, the results of the model should be robust to different values per kg for the three size classes as long as the values can be ranked in the same order, because the model maximizes the value of the landed catch. With availabilities of the three size classes similar to those in my simulation model, keeping more of the most valuable size class will still give a greater value to the landed catch, regardless of the magnitude of the differences between the values. However, if the values of the size classes became approximately equal, the stochastic nature of fishing would probably make it unlikely that fishermen would distinguish between them, and make high-grading less likely to occur.

The relative availability of the three size classes is not as important to high-grading behavior in my model as the absolute availability of the more valuable size classes. The important factor in the decision to high-grade is whether enough of the most valuable size class can be caught within the time constraints to justify discarding the other classes. Generally, as the more valuable size classes become more abundant, I would expect high-grading to become more common for any management regime. This was studied briefly in the simulation runs with higher and lower availabilities of fish that I discussed previously. However, my examination of the effects of fish availability on my results was limited; similar models should be built with fish availability estimates from other times or fisheries in order to make predictions about discarding behavior in those new situations.

Fixed costs, such as the travel costs of going to and from the fishing grounds, should have little effect on my results. They will only offset the final landed value of the catch by a fixed amount and will not change the fact that increased profit is expected from high-grading behavior. However, variable costs related to fishing activities, such as fuel costs while trawling or the risk of gear damage during a haul, could reduce the expected benefit of waiting for more valuable fish in future hauls. If the costs associated with making a haul exceed the expected value of a high-graded

haul, then high-grading will result in an economic loss for the haul and should not occur. Pikitch (1991) estimates vessel operating costs off the Oregon Coast as about \$36.42 per trawling hour. With an average of 4 or 5 hauls in a day, these variable costs are small relative to many of the values of the landings per trip being considered (Fig. 7e), but not relative to the those values for the cases where high-grading was most severe (at low TLLs and high TELs). Thus, the present model may overestimate high-grading behavior and the duration of trips when the limits on the amount of fish landed are low and the limits on effort are high. However, variable costs and the associated reduction in high-grading will not increase the profit from trips with low TLLs and high TELs, nor will variable costs have a large influence on behavior in situations where the gross profits are large.

Finally, the key assumption of my model, that fishermen maximize the value of their landed catch (profit), may be false. Alternatively, they may maximize their rate of profit (profitability or landed catch per unit effort) while fishing. In both cases I expect fishermen to attempt to maximize their profit over a season. My focus on the final landed value from a trip is similar to the assumption often made by fisheries economists, that "...for a fishing vessel, total revenue from a trip is more important than the marginal revenue created by a unit of output" (Doll 1988). There are also other financial strategies, such as minimizing potential losses, which could dominate the system and make high-grading less likely than my model would suggest. In addition to economic goals, it is possible that non-economic factors, such as the desire to be at sea, may play a role in determining the actual value of a fishing trip to fishermen, and result in economically suboptimal behavior (Smith 1974, 1981). Identifying the goals used by fishermen in a particular situation is an important step in applying any model of fishermen's behavior to a fishery. I have made an assumption that I feel is reasonable based upon available data, but a more detailed analysis with additional data would be required to show this.

## Conclusions

My model, though extremely simplified in relation to the processes it represents, still provides important insights into how fishermen's behavior may respond to management actions and produce undesirable, but potentially predictable, results. Presently, regulations that focus on fishing trips are becoming a common management tool (Pikitch 1991, Fisheries and Oceans Canada 1991), while concerns about the influence of discarding on the reliability of catch and effort data are leading to the development of statistical means of estimating it (e.g. Tallman 1990). However, evaluations of alternative management plans, and fisheries statistics in general, may be misleading if they do not include considerations of fishermen's behavior (Hilborn 1985, Lane 1988). Modeling behavior will never fully reflect the dynamic and complex conditions influencing fishery systems; thus models will never replace direct interactions by managers with members of the fleet. However, the value of a given method can only be measured by comparison to the other methods that are available. Presently, there is little formal methodology for the quantitative consideration of the effect of fishermen's behavior on the effectiveness of new regulations that can be used by management agencies. I suggest that explicitly evaluating the potential reactions of fishermen to management actions through modeling with the available data could be a better approach than current methods. If so, this will result in regulations that better achieve their goals while minimizing conflicts between managers and the fleet.

## Chapter 5

## General Conclusion

My results show that foraging theory can provide insightful, useful, and testable hypotheses for the study of fishing effort. Specifically, this thesis has shown that the analogy of a commercial fishing vessel to a predator can aid researchers in predicting the reactions of fishing fleets to changes in the abundance and distribution of fish, as well as their reactions to the regulations that management agencies might implement. In the second chapter, the ideal free distribution, from behavioral ecology, provides the theoretical basis for the prediction of the distribution of fishing effort in the Hecate Strait trawl fishery. The suitability of the ideal free distribution for the study of fishing effort suggests that CPUE may provide a poor index of abundance for a population when a fleet fishes among several spatially distinct populations. In the third and fourth chapters, high-grading in the sablefish component of the Oregon trawl fishery was examined from the perspective of diet choice theory, using dynamic programming. This approach allows the development of hypotheses about the response of fishermen's discarding behavior to diverse factors such as regulations, fish availability, and risk of injury or gear damage. In the fourth chapter, the use of this discarding model to examine the effect of different management regulations on high-grading clearly illustrates the potential utility of models that predict the behavioral responses of fishermen to changing conditions. Models of the behavior of fishermen, developed and tested with data from the fishery under scrutiny, will allow managers and researchers to improve both their interpretation of historical catch and effort data and their ability to foresee the potential outcome of future management actions.

In addition to its contribution to fisheries theory, my work adds to the field of behavioral ecology by extending the validity of the use of evolutionary paradigms for the prediction of animal behavior to new human situations, the B.C. and Oregon trawl fisheries, even though the link between the proximate currencies used (dollars) and the

ultimate evolutionary currency (genetic contribution to future generations) is not clearly definable. Additionally, the theoretical development in the third chapter indicates that diet choice decisions could arise solely from the constraint of gut capacity. This model of diet choice represents one extreme of a continuum of mechanisms; the original diet choice model based on foraging rate (Charnov 1976a, 1976b) is at the other extreme. Other models, such as Kaspari's (1990) or Houston and McNamara's (1985), contain elements of each mechanism. The combination of the two causes that lead to diet choice decisions will doubtlessly vary among the situations where this behavior is observed.

A single model of a trawl fishery, whose predictions encompassed the game theoretic aspects of the second chapter and the dynamic, state-dependent nature of the third and fourth chapters, could be developed using stochastic dynamic game theory (Mangel and Clark 1988). Such a model would allow the competitive interactions among fishing vessels (through interference and local prey depletion) to affect both the decision to high-grade and the spatial allocation of fishing effort. Dynamic game models have been proposed to deal with a variety of problems in behavioral ecology including habitat choice by juvenile salmon (*Oncorhynchus kitsutch*), oviposition decisions by tephritid flies (*Oriella ruficada*) (Mangel and Clark 1988), and singing to attract mates in passerine birds (Houston and McNamara 1987). The best decision that an individual can make in all of these cases was based upon its current state, the time, and the decisions being made by other individuals.

A dynamic game model of a trawl fishery could begin by focusing on the prediction of the spatial distribution of effort in order to replace the simpler ideal free distribution that I used in the second chapter. This model would then be expanded to include high-grading decisions. A general dynamic game model of habitat selection has already been proposed by Mangel (1990). His model allows the effects of risk, time, and the state of an individual to be included in the prediction of habitat choice, similar



to the manner that these factors were included in the prediction of high-grading decisions in the third and fourth chapters. In practice, the dynamic game algorithm attempts to converge on its solution by iterating through a series of dynamic program solutions and is therefore more computationally demanding than either an analytical game theoretic approach or an ordinary dynamic program. Also, a dynamic game may not converge on a solution, or if it does that solution may not be unique (Mangel 1990). More data than was available for this thesis would be required to develop a dynamic game model of a trawl fishery. For example, the availability of each type of fish in a haul would have to be estimated as a function of the local density of vessels and the previous local catch; this resolution was not available for the distribution of size classes in my model. Despite these problems, the potential for producing a unified model of fishing decisions makes dynamic games an obvious direction for future research.

There is still much room for development of all of the ideas presented in this thesis. In the first chapter, the identification of the source of competition effects in the Hecate Strait fishery remains unsolved. Here, additional observations would be required to resolve the relative contributions of interference and exploitation to the competition of vessels in the fishery. Clearly demonstrating the presence of interference is necessary to unequivocally establish the presence of an ideal free distribution in a fishery. The increasing levels of fishing effort that are common throughout the world's fisheries suggest that interference may be present in other fisheries, and that its role in the interactions of fishing vessels may be increasing. The application of my methodology to the spatial distribution of effort in other situations, and therefore the test of its generality, remains to be done. The additional study of other situations would also help to determine the generality of the high-grading model presented in the last two chapters. Even in the Oregon sablefish fishery, additional work will be required to precisely quantify the level of high-grading that is occurring because of the limited sample size that I used for the final test of high-grading.

Studies focusing on specific components of the catch of individual vessels require large temporal and financial investments by the agencies involved. Often, such expenditures require a priori justification. In this thesis, I have developed hypothesis tests and models based on data that are already available. Such an approach will be necessary in order to demonstrate the potential importance of more expensive research in fleet dynamics and to identify instances where this research is most likely to yield results.

### Appendix to Chapter 3

#### The simulation of the contents of a haul

The relationships among the three size classes, X, Y, and Z, described in the Methods section of chapter 3 were used to generate haul contents in the following manner. Each simulated haul began with a choice of the amount of Z caught, drawn from the true data. Then the probability of Y being absent from the haul was calculated using a logit model with the simulated amount of Z as the independent variable. Then a number between 0 and 1 was randomly chosen from a uniform distribution. The Y value was set to zero when this number was less than the calculated probability of Y being absent in the haul. Otherwise, the amount of Y caught was calculated from the logarithmic regression equation, once again using the amount of Z as the independent variable. Finally, a residual value, chosen randomly from the regression of the original data, was added to the predicted Y value in order to simulate the natural stochastic variability of the data. A similar procedure was performed to simulate X in the haul, using both Z and Y as predictor variables.

## Bibliography

- Abrahams, M.V. and L.M. Dill. 1989. A determination of the energetic equivalence of the risk of predation. *Ecology* 70: 999-1007.
- Abrahams, M.V. and M.C. Healey. 1990. Variation in the competitive abilities of fishermen and its influence on the spatial distribution of the British Columbia salmon troll fleet. *Can. J. Fish. Aquat. Sci.* 47: 1116-1121.
- Allen, P.M. and J.M. McGlade. 1986. Dynamics of discovery and exploitation: the case of the Scotian Shelf groundfish fisheries. *Can. J. Fish. Aquat. Sci.* 43: 1187-1200.
- Andersen, R. 1973. Those fishermen lies: custom and competition in North Atlantic fishermen communication. *Ethnos* 73: 153-164.
- Argue, A.W., R. Hilborn, R.M. Peterman, M.J. Staley and C.J. Walters. 1983. Strait of Georgia Chinook and coho fishery. *Can. Bull. Fish. Aquat. Sci.* No. 211. 91 p.
- Beauchamp, G., M. Guillemette and R. Ydenberg. 1992. Prey selection while diving by common eiders, *Somateria mollissima*. In press. *Anim. Behav.*
- Bellman, R. 1957. Dynamic programming. Princeton University Press. Princeton, NJ, 339 p.
- Belovsky, G.E. 1978. Diet optimization in a generalist herbivore: the moose. *Theor. Pop. Biol.* 14: 105-134.
- Box, G.E.P. and G.S. Watson. 1962. Robustness to non-normality of regression tests. *Biometrika* 49: 93-106.
- Caddy, J.F. 1982. Management of Shrimp Fisheries. p. 120-123. *In* Fish by-catch - bonus from the sea: report of a technical consultation on shrimp by-catch utilization held in Georgetown, Guyana, 27-30 October 1981. Ottawa, Ont. IDRC.

- Charles, A.T. 1989. Bio-socio-economic fishery models: labour dynamics and multi-objective management. *Can. J. Fish. Aquat. Sci.* 46: 1313-1322.
- Charnov, E.L. 1976a. Optimal foraging: attack strategy of a mantid. *Am. Nat.* 110: 141-151.
- Charnov, E.L. 1976b. Optimal foraging: the marginal value theorem. *Theor. Popul. Biol.* 9: 129-136.
- Clark, C.W. 1985. Bioeconomic modelling and fisheries management. John Wiley and Sons, Toronto. 291 p.
- Clark, C.W. 1987. The lazy, adaptable lions: a Markovian model of group foraging. *Anim. Behav.* 35: 361-368.
- Clark, C.W. and M. Mangel. 1979. Aggregation and fishery dynamics: a theoretical study of schooling and the purse seine tuna fisheries. *Fish. Bull., U.S.* 77: 317-337.
- Clark, C.W. and M. Mangel. 1983. Uncertainty, search and information in fisheries. *J. Cons. Int. Explor. Mer* 41: 93-103.
- Cook, R.M. and B.J. Cockrell. 1978. Predator ingestion rate and its bearing on feeding time and the theory of optimal diets. *J. Anim. Ecol.* 47: 529-547.
- Cook, R.M. 1984. Evidence for directed fishing effort in North Sea cod and haddock stocks. *J. Cons. Int. Explor. Mer* 41: 199-204.
- Cooke, J.G. 1985. On the relationship between catch per unit effort and whale abundance. *Rep. Int. Whal. Comm.* 35: 511-519.
- Crittenden, R.N. and G.L Thomas. 1989. A conditional generalized least squares method for estimating the size of a closed population. *Can. J. Fish. Aquat. Sci.* 46: 818-823.
- Deriso, R.B., T.J. Quinn and P.R. Neal. 1985. Catch-age analysis with auxiliary information. *Can. J. Fish. Aquat. Sci.* 42: 815-824.

- Dixon, W.J. and F.J. Massey, Jr. 1969. Introduction to statistical analysis. 3rd ed. McGraw Hill Book Co., New York. 638 p.
- Doll, J.P. 1988. Traditional economic models of fishing vessels: a review with discussion. *Mar. Res. Econ.* 5: 99-123.
- Draper, H.N.R. and H. Smith. 1981. Applied regression analysis. 2nd. ed. John Wiley and Sons Ltd., New York. 709 p.
- Eales, J. and J.E. Wilen. 1986. An examination of fishing location in the pink shrimp fishery. *Mar. Res. Econ.* 2: 331-351.
- Emlen, J.M. 1966. The role of time and energy in food preference. *Am. Nat.* 100: 611-617.
- Fisheries and Oceans Canada. 1990. 1991 Atlantic groundfish multi-year management plan (1991-1993). 114 p.
- Fisheries and Oceans Canada. 1991. Pacific groundfish trawl management plan 1992. 30 p.
- Foley, R. 1985. Optimality theory in anthropology. *Man* 20: 222-242.
- Fretwell, S.D. 1972. Populations in a seasonal environment. Princeton University Press, Princeton, New Jersey. 217 p.
- Fretwell, S.D. and H.L. Lucas. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheor.* 19: 16-36.
- Garcia, S. 1988. Tropical penaeid prawns, p. 219-250. *In* Gulland, J.A. [ed.] Fish population dynamics. 2nd ed. John Wiley and Sons, New York, NY.
- Gillis, D.M. and D.L. Kramer. 1987. Interference ideal free distributions: population density and patch use by zebrafish. *Anim. Behav.* 35: 1875-1882.
- Giraldeau, L.A. and D.M. Gillis. 1988. Do lions hunt in group sizes that maximize hunter's daily food returns? *Anim. Behav.* 36: 611-613.

- Godin, J.G. and M.H.A. Keenleyside. 1984. Foraging on patchily distributed prey by a cichlid fish (Teleostei, Cichlidae): a test of the ideal free distribution theory. *Anim. Behav.* 32: 120-131.
- Goss-Custard, J.D. 1980. Competition for food and interference among waders. *Ardea* 68: 31-52.
- Gulland, J.A. 1974. The management of marine fisheries. University of Washington Press, Seattle, WA. 198 p.
- Halliday, R.G., D.E. Hay, and K.I. Metuzals. 1989. Wastage of American plaice (*Hippoglossoides platessoides* (Fabricus)) in the southern Gulf of St. Lawrence fishery in the 1970's. *Can. Tech. Rep. Fish. Aquat. Sci.* 1663: 36 p.
- Hames, R.B. and W.T. Vickers. 1982. Optimal diet breadth as a model to explain variability in Amazonian hunting. *Am. Ethnol.* 9: 258-278.
- Harper, D.G.C. 1982. Competitive foraging in mallards: 'ideal free' ducks. *Anim. Behav.* 30: 575-584.
- Hawkes, K., K. Hill and J.F. O'Connell. 1982. Why hunters gather: optimal foraging and the Ache of eastern Paraguay. *Am. Ethnol.* 9: 379-398.
- Hawkes, K. and J.F. O'Connell. 1985. Optimal foraging models and the case of the !kung. *Am. Anthropol.* 87: 401-405.
- Hayman, R.A., A.V. Tyler and R.L. Demory. 1980. A comparison of cohort analysis and catch per unit effort for Dover sole and English sole. *Trans. Amer. Fish. Soc.* 109: 35-55.
- Hilborn, R. 1985. Fleet dynamics and individual variation: why some people catch more fish than others. *Can. J. Fish. Aquat. Sci.* 42: 2-13.
- Hilborn, R. and M. Ledbetter. 1979. Analysis of the British Columbia salmon purse-seine fleet: dynamics of movement. *J. Fish. Res. Board Can.* 36: 384-391.
- Hilborn, R. and R.B. Kennedy. A general theory of fishermen's movement and CPUE. Unpublished manuscript.

- Hill, K. 1988. Macronutrient modifications of optimal foraging: an approach using indifference curves applied to some modern foragers. *Human Ecol.* 16: 157-197.
- Hoag, S.H. 1975. Survival of halibut released after capture by trawls. International Pacific Halibut Commission, Scientific Report no. 57. 18 p.
- Holling, C.S. 1966. The functional response of invertebrate predators to prey density. *Mem Entomol Soc Canada* 48: 1-86.
- Houston, A. and J. McNamara. 1985. The choice of two prey types that minimizes the probability of starvation. *Behav. Ecol. Sociobiol.* 17: 135-141.
- Houston, A. and J. McNamara. 1987. Singing to attract a mate: a stochastic dynamic game. *J. Theor. Biol.* 129: 57-68.
- IPHC (International Pacific Halibut Commission). 1991. Annual Report, 1990. 52 p.
- Johnson, D.M., B.G. Akre and P.M. Crowley. 1975. Modeling arthropod predation: wasteful killing by damselfly naiads. *Ecol.* 56: 1081-1093.
- Kaspari, M. 1990. Prey preparation and the determinants of handling time. *Anim. Behav.* 40: 118-126.
- Keeney, R.L and H. Raiffa. 1976. Decisions with multiple objectives: preferences and value tradeoffs. John Wiley and Sons, New York, NY. 569 p.
- Krebs, J.R. and N.B. Davies. 1984. Behavioral ecology: an evolutionary approach. 2nd ed. Blackwell Scientific Publications, Oxford, U.K. 493 p.
- Krebs, J.R., J.T. Erichsen, M.I. Webber and E.L. Charnov. 1977. Optimal prey selection in the great tit (*Parus major*). *Anim. Behav.* 25: 30-38.
- Kulka, D.W. and S.C. Stevenson. 1986. Trends in discarding of divisions 2J3KL cod by the Newfoundland offshore fleet for 1981-1986, with particular reference to size of fish. CAFSAC Res. Doc. 86/101. 19 p.
- Lane, D.E. 1988. Investment decision making by fishermen. *Can. J. Fish. Aquat. Sci.* 45: 782-796.



- Lane, D.E. 1989. A partially observable model of decision making by fishermen. *Opns. Res.* 37: 240-254.
- Lapointe, M.F. 1989. Numerical and functional responses of British Columbia trawler fishermen. M.Sc. thesis, University of British Columbia, Vancouver. 319 p.
- Larkin, P.A. 1977. An epitaph for the concept of maximum sustained yield. *Trans. Am. Fish. Soc.* 106: 1-11.
- Lima, S.L. and L.M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68: 619-640.
- Lucas, J.R. and Grafen A. 1985. Partial prey consumption by ambush predators. *J. Theor. Biol.* 113: 455-473.
- Mangel, M. 1990. A dynamic habitat selection game. *Math. Biosci.* 100: 241-248.
- Mangel, M. and C.W. Clark. 1988. *Dynamic modeling in behavioral ecology.* Princeton University Press. Princeton, NJ. 308 p.
- May, R.M. [ed.] 1984. *Exploitation of marine communities.* Springer-Verlag, Berlin. 366 p.
- McCay, B.J. 1978. Systems ecology, people ecology, and the anthropology of fishing communities. *Human Ecology* 6: 397-423.
- McCay, B.J. 1981. Optimal foragers of political actors? Ecological analysis of a New Jersey fishery. *Am. Ethnol.* 8: 356-382.
- Milinski, M. and Parker G.A. 1991. Competition for resources, p. 137-168. *In* Krebs, J.R. and N.B. Davies [ed.] *Behavioral Ecology: an evolutionary approach*, 3rd ed. Blackwell Scientific Publications, Oxford, U.K.
- Millington, P. 1984. The fishermen as predator: numerical responses of British Columbia gillnet fishermen to salmon abundance. M.Sc. Thesis, University of British Columbia, Vancouver. 93 p.
- Orbach, M.K. 1977. *Hunters, seamen and entrepreneurs. The tuna seinermen of San Diego.* Univ. Cal. Press, Berkeley, CA. 304 p.

- Paloheimo, J.E. and L.M. Dickie. 1964. Abundance and fishing success. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 155: 152-163.
- Peterman, R.M. and G.J. Steer. 1981. Relation between sport-fishing catchability coefficients and salmon abundance. Trans. Amer. Fish. Soc. 110: 585-593.
- Peterman, R.M., G.J. Steer and M.J. Bradford. 1985. Density dependent catchability coefficients. Trans. Amer. Fish. Soc. 114: 436-440.
- Pikitch, E.K. 1987. Impacts of management regulations on the catch and utilization of rockfish in Oregon. Proceedings of the international rockfish symposium, University of Alaska Sea Grant Report 87-2: 369-382.
- Pikitch, E.K. 1988. Objectives for biologically and technically interrelated fisheries, p. 107-135. In Wooster, W.S. [ed.] Fishery science and management. Springer-Verlag, New York, NY.
- Pikitch, E.K. 1991. Technological interactions in the US west coast groundfish trawl fishery and their implications for management. ICES mar. Sci. Symp. 193: 253-263.
- Pikitch, E.K., D.L. Erickson and J.R. Wallace. 1988. An evaluation of the effectiveness of trip limits as a management tool (preliminary report). NWAFC processed report 88 - 27, NOAA, U.S. Department of Commerce, 33 p.
- Powles, P.M. 1969. Size changes, mortality, and equilibrium yields in an exploited stock of American plaice (*Hippoglossoides platessoides*). J. Fish. Res. Board Canada 26: 1205-1235.
- Pulliam, R.H. 1974. On the theory of optimal diets. Am. Nat. 108: 59-75.
- Rice, W.R. 1989. Analyzing tables of statistical tests. Evolution 43: 223-225.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: 382 p.

- Ricker, W.E. 1976. Review of the rate of growth and mortality of Pacific salmon in salt water, and noncatch mortality caused by fishing. *J. Fish. Res. Board Can.* 33: 1483-1524.
- Roff, D.A. and D.J. Fairbairn. 1980. An evaluation of Gulland's method for fitting the Schaefer model. *Can. J. Fish. Aquat. Sci.* 37: 1229-1235.
- Rothschild, B.J. 1977. Fishing effort. p. 96-115. *In: J.A. Gulland [ed.] Fish population dynamics.* John Wiley and Sons Ltd., Toronto.
- Saila, S.B. 1983. Importance and assessment of discards in commercial fisheries. *FAO Fish Circ (765).* 62 p.
- Seigel, S. 1956. *Nonparametric statistics for the behavioral sciences.* McGraw-Hill, New York. 312 p.
- Sih, A. 1980. Optimal foraging: partial consumption of prey. *Am. Nat.* 116: 281-290.
- Sih, A. and K.A. Milton. 1985. Optimal diet theory: should the !kung eat mongongos. *Am. Anthropol.* 87: 396-401.
- Slavin, J.W. 1982. Utilization of the shrimp by-catch. p. 21-28. *In Fish by-catch - bonus from the sea: report of a technical consultation on shrimp by-catch utilization held in Georgetown, Guyana, 27-30 October 1981.* Ottawa, Ont. IDRC.
- Smith, C.L. 1974. Fishing Success in a regulated commons. *Ocean Development and International Law Journal.* 1: 369-382.
- Smith, C.L. 1980. Management provoked conflicts in the fisheries. *Env. Mgt.* 4: 7-11.
- Smith, C.L. 1981. Satisfaction bonus from salmon fishing: implications for economic evaluation. *Land Economics* 57: 181-194.
- Smith, C.L. and R. McKelvey. 1986. Specialist and generalist: roles for coping with variability. *N. Amer. J. Fish. Mgmt.* 6: 88-99.
- Smith, C.L., J.M. Stander and A.V. Tyler. 1982. Human behavior incorporated into ecological computer simulations. *Envir. Mgmt.* 6: 251-260.

- Smith, E.A. 1983. Anthropological applications of optimal foraging theory: a critical review. *Curr. Anthropol.* 24:625-651.
- Sokal, R.R. and F.J. Rohlf. 1981. *Biometry*. 2nd ed. W.H. Freeman and Co., New York, NY. 859 p.
- Statistics Canada. 1980. Consumer prices and price indexes. 5. 120 p.
- Statistics Canada. 1982. Consumer prices and price indexes. 7. 120 p.
- Statistics Canada. 1991. Consumer prices and price indexes. 16. 120 p.
- Stephens, D.W. and J.R. Krebs. 1986. *Foraging theory*. Princeton University Press, Princeton, NJ. 247 p.
- Talbot, A.J. and D.L. Kramer. 1986. Effects of food and oxygen availability on habitat selection by guppies in a laboratory environment. *Can. J. Zool.* 64: 88-93.
- Tallman, R. 1990. Reduction of uncertainty caused by discarding in the fisheries of the gulf of St. Lawrence. *NAFO Sci. Coun. Studies*, 16: 39-48.
- Thompson, R.E. 1981. Oceanography of the British Columbia Coast. *Can. Spec. Publ. Fish. Aquat. Sci.* 56: 291 p.
- Wardle, C.S. 1986. Fish behavior and fishing gear, p. 463-495. *In*: Pitcher, T.J. [ed.] *The behavior of teleost fishes*. Croom Helm Ltd., Beckenham, U.K.
- Westrheim, S.J. 1983. A new method for allotting effort to individual species in a mixed-species trawl fishery. *Can. J. Fish. Aquat. Sci.* 40: 352-360.
- Whitham, T.G. 1980. The theory of habitat selection: examined and extended using *Pemphigus* aphids. *Amer. Nat.* 115: 449-466.
- Wilkinson, L. 1989. *SYSTAT: The system for statistics*. SYSTAT, Inc., Evanston, IL. 822 p.
- Wooster, W.S. 1988. Biological objectives of fisheries management, p. 1-6. *In* Wooster, W.S. [ed.] *Fishery science and management*. Springer-Verlag, New York, NY.