

**Numerical and Functional Responses
of British Columbia Trawlers**

by

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Abstract

Numerical responses were examined in the movement of trawlers among seven aggregate fishing areas off the British Columbia coast. Three hypotheses for movement patterns were tested: (1) Movement follows traditional patterns, (2) Movement equalizes the gross dollar returns to effort (LPE\$) in each area, and (3) Movement maintains relative LPE\$ in each area. On the interannual time scale, I rejected the Equalize LPE\$ hypothesis, but failed to reject either the Traditional Patterns or Maintain Relative LPE\$ hypothesis. On the intra-annual time scale, I rejected both LPE\$ hypotheses, but was unable to reject the Traditional Patterns hypothesis; although traditional movement patterns were evidently being modified by changes in the timing of LPE\$ in all the areas and by fishing regulations in two of the seven areas. Three assumptions of the Equalize LPE\$ hypothesis were violated, and accounting for violations (especially assumptions concerning movement and areas specific costs) would result in smaller differences in LPE\$ between areas and between years within areas. Numerical responses have implications for anticipating the responses of fishing fleets to changes in regulations and for evaluating changes in the economic benefits of alternative fishing areas.

Functional responses were examined in a multispecies fishery in Hecate Strait. Two similar techniques for estimating the abundance of exploited fish populations were compared: (1) Virtual Population Analysis (VPA) and (2) Catch-at-age analysis with auxiliary information (CAGEAN). Estimates for each of three species (Pacific cod, English sole, and rock sole) from both techniques were sensitive to the choice of natural mortality rate but insensitive to the choice of fishing mortality rate. In most cases, abundance and catchability estimates from

alternative input parameters were highly correlated and had very similar time trends. Similar time trends in estimates were also obtained from the two techniques when the best estimates of input parameters were used. Estimates of abundances, catchabilities and catch per predator from both techniques were used to examine functional responses of trawlers to fish abundance.

I compared the fit of three alternative single species functional response models: (1) a linear model (type I), (2) a saturating model (type II), and (3) a generalized equation that could mimic four different responses (types I-IV) depending on its parameter values. The generalized equation predicted sigmoid (type III) functional responses for 11 of the 12 data sets. However, only 5 of the model comparisons were statistically significant; all five indicated that a sigmoid response was most consistent with the data. Single species mortality models fit most data sets poorly, although in most cases, the form of the mortality curve was consistent with the corresponding functional response.

I also fit two alternative multispecies functional response models and examined one mechanism, switching, that could result in type III responses. Multispecies functional response and mortality models often resulted in much better fits than single species models for each species. I failed to detect switching in any of the data sets, although the power of the tests of the switching hypothesis was low in most cases. Type III functional responses and multispecies functional responses have implications for: (1) interpretations of abundance indices based on catch per unit of fishing effort, (2) equilibrium yield vs. abundance or harvest rate relationships and (3) simulation models used to evaluate alternative harvest strategies.

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General Introduction

Predators can exhibit two types of responses to changes in density of their prey: (1) functional responses and (2) numerical responses (Solomon 1949). Numerical responses describe how the number of predators changes with prey density. The change in the number of prey eaten per predator with changes in prey (or predator) density is the functional response. Numerical responses can be further divided into two types; a short term aggregation of predators in response to changes in prey density in space and/or time, and a longer term reproductive response of predators to changes in abundance of prey.

Recent studies have found that fishermen have numerical and functional responses akin to those described by Solomon for natural predators (e.g. Hilborn and Ledbetter 1979; Millington 1984; Peterman et al. 1979; Peterman 1980; Peterman and Steer 1981). These studies, and others, have demonstrated that applying theories for natural predators to fishermen is a viable approach that has implications for fisheries management.

The potential importance of studying fishermen as predators was outlined by Hilborn (1985) who argued that fisheries management is largely managing fishermen, and that a failure to understand fishermen as predators was a source of many fisheries management problems. Thus he proposed that more research in fisheries should be focused on the interactions among fish populations, fishermen, processors and markets. Hilborn (1985) focused particular emphasis on the study of fishermen as predators which he called *fleet dynamics*. He divided fleet dynamics into four components (1) investment and fleet size, (2) effort allocation (3) harvest efficiency, and (4) discarding and by-catch.

Investment and fleet size are analogous to growth and reproduction in natural predators (i.e. the reproductive numerical response of Solomon above). The lack of understanding of the processes that motivate fishermen to invest in some years but not in others has resulted in an inability to curb overinvestment which is rampant among fishing fleets throughout the world (e.g. Pearse 1982; Kirby 1982; Meuriot 1986). The net results of overinvestment are the same problems that result when there are too many natural predators: (1) excessive pressure on the prey population (creating a conservation problem for the fisheries manager), and (2) inefficient use of the resource (causing economists concern over "dissipation of potential resource rents"; e.g. Gordon 1954). These problems are particularly exacerbated in the fishery because unlike populations of natural predators that usually decline after overharvesting a resource, fishermen are often aided by "supplemental food" in the form of subsidies, loans and unemployment insurance designed to help fishermen survive when prey are in short supply (e.g. Davis and Thiessen 1986). Furthermore, unlike natural predators which must slowly evolve more efficient capture methods, successful fishermen can buy many devices that immediately increase their capture success (e.g. various electronic fish finders).

Hilborn (1985) defined effort allocation as the choice of time, location and species to catch. Understanding effort allocation is important for anticipating short (e.g. weekly) and long term (e.g. annual) shifts in effort patterns in response to changes in regulations, markets, or fishing opportunities created by managers (e.g. salmon enhancement; Hilborn and Ledbetter 1979).

Harvest efficiency relates catch per predator to abundance (i.e. the functional response), and to vessel characteristics (e.g. length, engine horsepower). The form of the functional response has obvious importance because in most

fisheries catch per predator is used as an index of the abundance of fish. Knowledge of the determinants of catching power is useful in standardizing predators (e.g. fishing vessels) so that indices of abundance can be adjusted for changes in catching power over time that occur due to changes in fleet composition (e.g. Robson 1966; Kimura 1981).

Fishermen are profit motivated, and because the cost of rejecting prey is usually small, they generally only keep the most valuable species. Thus discarding is a major problem in fisheries. Discarding makes it extremely difficult to assess the impact of fishing on nontarget or by-catch species, because: (1) a significant proportion of discarded fish die, (2) the discarded catch of these species is usually not observed, and (3) estimation of discarded catch is difficult.

Thus, the motivation for the thesis came from two principal sources. First, I was curious about the theories of functional and numerical responses of predators, and fishermen provided an interesting case study. Second, examining the responses of fishermen as predators provided an opportunity to consider some practical implications of the theories of natural predators for fisheries assessment and management. Specifically, the thesis focuses on two main topics. The first part investigates the numerical responses of the British Columbia trawl fleets to the relative abundance of prey (measured in dollar value). The second part investigates the functional responses of trawlers to the abundance of three species caught in Hecate Strait, an area of particularly rich fishing grounds located between the Queen Charlotte Islands and British Columbia's northern mainland. The organization of each of these parts is detailed below.

I. Numerical Responses

The first part consists of Chapters 1-4. Chapter 1 is a literature review of numerical response studies in fisheries. Four alternative approaches are reviewed: (1) models of fisherman's choice, (2) applications of search theory and optimization, (3) simulation models, and (4) empirical examinations of fisheries data sets. Each of these approaches is examined in terms of its strengths and weaknesses.

Chapter 2 investigates three alternative hypotheses proposed by Hilborn and Ledbetter (1979) to explain movement patterns of salmon seine fishermen that may describe patterns in the numerical responses of the trawl fleet. Because of the multispecies nature of the trawl fishery, and the assumption that fishermen are profit motivated, I used the landed value of the catch per days fished (LPE\$) as a surrogate for fish abundance. The hypotheses examined are (1) movement follows traditional (i.e. historical) patterns, (2) vessels move to equalize LPE\$ among alternative fishing areas, and (3) vessels move to maintain relative LPE\$ among areas (i.e. some areas will have consistently higher LPE\$ than others relative to the coastwide average LPE\$ for all areas). The hypotheses were examined on and inter- and intra-annual time scale and a fixed spatial scale that divided the British Columbia coast into 7 fishing areas.

Chapter 3 investigates some of the assumptions of the Hilborn and Ledbetter (1979) hypotheses and considers what effects potential violations of these assumptions may have had on the results of Chapter 2. The evaluation of assumptions varies from drawing on existing literature sources to detailed analyses depending on the available data.

Chapter 4 discusses the previous three chapters. The discussion first focuses on a comparison of the results from my study with the results from Hilborn and Ledbetter (1979) and Millington (1984) who examined the Hilborn and Ledbetter (1979) hypotheses using data for salmon gillnet fishermen. Next, I discuss some problems with data sets and statistical issues common to examinations of numerical responses in fisheries are mentioned. I conclude with some general implications of numerical responses.

II. Functional Responses

The second part comprises Chapters 5-8. Chapter 5 reviews the literature for functional response in natural predators, to provide the foundation for examination of functional responses in the fishery. Particular emphasis is placed on four alternative functional response types, their equations, and potential mechanisms . .

Chapter 6 reviews the literature on functional responses in the fisheries. Few fisheries studies endeavored to explicitly examine functional responses, but many studies have implications for functional responses. In order to draw analogies between natural predators and fishermen, Chapter 6 follows a parallel organization to Chapter 5.

Estimates of abundance are required for any examination of functional responses. Thus, Chapter 7 examines two similar methods for estimating the abundance of exploited fish populations from data on the age composition of catches gathered over time. Each technique is reviewed in terms of its data requirements, underlying model and assumptions. The two techniques are then applied to data for three species caught in Hecate Strait, and abundance

estimates from the two techniques are compared. In addition, I evaluate the sensitivity of estimates from each technique to alternative input parameters (fishing and natural mortality rates).

Chapter 8 examines the functional responses of trawlers to the abundance of Pacific cod, English sole and rock sole, which are the major components of a multispecies trawl fishery in Hecate Strait. Firstly, I fit three alternative functional response models and their corresponding mortality curves to the data from each of the three species. Secondly, I consider two alternative multispecies functional response models in attempt to model the three species system as a whole. Thirdly, I examine one mechanism for functional responses in the fishery (switching; Murdoch 1969).

The discussion, covering Chapters 5-8, considers outstanding statistical and biological issues and presents some general implications of the findings for fisheries.

Chapter 1: Literature review of Numerical Responses in Fisheries

Introduction

While studies of numerical responses of animal predators have focused on the implications of responses for the total predator-prey system (eg. Beddington et al. 1976), the application of numerical responses to fishing systems has generally taken a different approach for two reasons. First, the analogous processes to reproductive responses in fisheries are changes in fleet size, and/or investments in improved catching power. Because of the economic nature of these responses, studies tended to focus on economic rather than biological implications (eg. Clark et al. 1979, Aranson 1984, Charles 1983, Charles and Munro 1985, Lane 1988). Second, estimates of absolute abundance are rarely available in commercial fisheries, and when estimates are available they generally have poor precision. Thus, most applications of numerical responses to fishing systems have focused on short term aggregation responses, and the implications of fleet movement patterns.

In this chapter I review some alternative approaches to numerical response studies that have been applied to fisheries. I have grouped my review of alternative approaches into four main categories: (1) models of fisherman's choice, (2) applications of search theory and optimization, (3) simulation models, and (4) empirical studies of particular fisheries. For each category, I first briefly review the technique, then highlight studies that have applied the technique, and finally comment on the technique's strengths and weaknesses.

Models of Fisherman's Choice

A few studies have applied a method known as logit analysis to the examination and prediction of discrete choice behavior by fishermen. Logit analysis relates discrete choices to a number of discrete or continuous explanatory variables (Swierzbinski 1985). For example, the discrete choice of fishing location could be related to the continuous explanatory variable LPE\$ (landed value of the catch per unit of fishing effort), and a discrete explanatory variable such as risk of gear damage (classified as high, medium, or low). Other typical discrete choices made by fishermen include gear type and target species.

More specifically, the logit model relates the probability of choosing a particular alternative (e.g. area to fish) to the explanatory variables. Swierzbinski (1985) gives the formulation for the two choice logit model as

$$P(j|X_i) = \exp(a_0 + \sum b_i X_i) / (1 + \exp(a_0 + \sum b_i X_i)) \quad (1.1)$$

where $P(j|X_i)$ is the probability of choosing the alternative j (e.g. an area) given X_i (e.g. the areas LPE\$ and risk of gear damage), \sum is the sum over explanatory variables, and a_0 and b_i are constants to be estimated. For more details on choice models see Maddala (1983), Swierzbinski (1985) and the references therein.

Eales and Wilen (1986) used the logit model to predict area choice in the California pink shrimp trawl fishery. Using expected catch and distance from home port as explanatory variables, they were able to predict the location of the first set of the day correctly 90% of the time for 3 aggregate areas, and 55%

of the time for 8 smaller areas. The study demonstrated that fishermen are influenced on short time scales (i.e. daily) by relative abundance information, and the authors suggested economic inefficiencies may result from excessive movement into apparently profitable areas.

The logit model was used to predict fishery choice by New England fishermen by Bockstael and Opaluch (1983) (see also Opaluch and Bockstael 1984). Alternative fishery choices included scalloping from New Bedford, otter trawling from southern New England ports, and shrimping from Maine ports. The explanatory variables included the expected net returns, initial wealth, and a variable that measured the resistance to changing fisheries. They concluded fishermen respond to economic incentives of expected returns and variability in returns, but only after these incentives surpass a substantial threshold.

The strength of the logit model approach is its consideration of the behavior of individual fishermen or fishing units. The economists who have applied the approach argue that it is preferable to approaches that deal with aggregate data because the method is applied at the core of the common property nature of fisheries (i.e. decisions by individuals). One weakness of the logit model is that the explanatory variables such as "expected returns" are not observed, but instead must be estimated using proxies such as average catch in a previous time period. This can be a difficult task since catches in subsequent time periods may not be correlated (e.g. Eales and Wilen 1986). Furthermore, expected catches and profits will depend on information flow, that may depend on many nonquantifiable factors. These problems may limit the situations where the logit model can be applied. Swierzbinski (1985) stated that the logit model is not appropriate when the choices are close substitutes, and discussed the appropriate statistical properties and conditions for applying the logit model. More details are

also provided in Bockstael and Opaluch (1983) and Eales and Wilen (1986).

Applications of Search Theory and Optimization

A second approach to the study of movement dynamics has been to apply aspects of the theory of search to fishermen's decisions. This approach casts the choices facing fishermen in a formal decision making setting and considers how fishermen should respond given an assumed probability of encountering fish (e.g. at a particular location and/or time) and a specified goal of the fishing enterprise (e.g. maximize catch). Thus, the application of search theory has two basic steps: (1) choosing the empirical distribution for the probability of encountering fish (usually clumps or schools of a uniform size), and (2) applying decision rules that describe what to do given a probability of encountering fish.

The choice of the probability distribution in step 1 depends on the spatial distribution of fish. The Poisson distribution is appropriate when fish are distributed randomly, but the Negative Binomial distribution is more appropriate when fish are distributed in patches or schools (Swierzbinski 1985). Decision rules depend on the goals of the fishing enterprise. Applications of search theory to movement studies have generally been concerned with the optimal patterns of effort allocation given particular choices for steps 1 and 2.

Shotton's (1973) work provided the foundation for much of the more recent applications of search theory to fishing systems. Shotton was one of the first to consider possible distributions for fish schools. He fit several alternative types of distributions to transect data on albacore tuna¹ gathered by research

¹ All common names of fishes used follow the American Fisheries Society convention (AFS, 1980).

vessels using troll gear (from Craig and Graham 1961). Of the five distributions he considered, the Negative binomial distribution fit the data best.

Shotton's second contribution was the application of Bayes' theorem to make predictions about how expected fish density changed in relation to fishing strategies. The premise for Bayes' theorem is to make expected fish density at any given time depend on two factors: 1. prior sample results (e.g. preseason sampling such as the albacore tuna transects), and 2. current catches as the fishing season progresses. More specifically, Bayes' theorem states

$$P(\lambda|x_i) \propto P(x_i|\lambda)P(\lambda) \quad (1.2)$$

where λ is the population density over the fishing grounds, x_i is the sample results or catches, $P(\lambda|x_i)$ is the probability of λ given the sample data (called the posterior probability), $P(x_i|\lambda)$ is the likelihood of obtaining the sample data if λ is the actual fish density, and $P(\lambda)$ is the prior probability of λ being the fish density (from Lindley 1965, cited in Shotton 1973).

Shotton applied the Bayes' formulation to a situation where the objective of the fishing decision was to minimize the loss due to changing grounds unnecessarily. The loss due to changing grounds, L_c , was given by

$$L_c = k(t\lambda + t_i(\lambda-\psi)) \quad (1.3)$$

where k is a proportionality constant, t is the time to change grounds, λ is the actual fish density on the present ground, t_i is the time to "make a trip" on the alternative ground, and ψ is the expected catch rate on the alternative ground. Given the formula for expected loss, the albacore tuna data, and an example of two alternative grounds, he derived formulae for determining when it

was best to change grounds.

Shotton also applied search theory to the British Columbia trawl fishery, that he characterized as having grounds where fish are either practically absent, or present in acceptable quantities. He determined the sequence in which three fishing grounds should be fished under two conditions. In the first case he ignored seasonal changes and assumed the probabilities of encountering fish and time to determine presence or absence were equal in each of the areas. The best strategy was the one with the lowest possible costs (time to cover the fishing ground plus steaming times to and from port). In the second case he allowed for different probabilities of encountering fish and assumed the time to detect presence or absence was proportional to the relative size of each ground and gave the necessary conditions (relative probabilities of encounter) for each sequence to be best in terms of minimizing the relative loss.

Other studies also used Shotton's approach. For example, Mangel and Clark (1983) applied search theory to two similar problems. The first considered the optimal allocation of search effort over two fishing ground where the current abundance of fish was assumed to have some known (prior) probability distribution (as in step 1 above). The second problem considered the optimal allocation of vessels over time to one ground. In each problem, new information on catch rates during the season affected the expected probabilities of encountering fish in subsequent time periods, and dynamic programming was used to solve for the optimal decisions. The authors assumed an objective of maximization of the total net seasonal revenue equal to the total value of the catch minus the costs of movement between grounds.

The conclusions of the first part of the study were: (1) information obtained from sampling of fish stock can lead to significant increases in expected catches, (2) the amount of information obtained depends on the initial allocation of vessels, and (3) the exact allocation may not be critical, provided some searching takes place on each ground (Mangel and Clark 1983). The second part of the study compared the strategies, of complete cooperation and complete competition among vessels. The cooperative strategy followed the optimal allocation determined from the model, while the competitive strategy allocated all vessels to fish in the first period. The competitive strategy performed progressively worse as the total number of vessels in the fishery increased (Mangel and Clark 1983).

There are two major strengths of the search theory applications. First, the probability of encounter is associated explicitly with an assumed spatial distribution of fish. Second the use of Bayes' theorem has some intuitive appeal because it mimics processes that occur in real life fisheries: formulation of prior expectations and updating as more information becomes available (e.g. catches). Prior probabilities can be based on preseason surveys, or on the judgement of skippers if data are lacking. Updating of these preseason expectations occurs through catches obtained as the season progresses. It is unlikely that fishermen use such a formal process in making their decisions, but the concepts of prior expectations and updating certainly apply.

While some aspects of search theory applications have intuitive and theoretical appeal, there are weaknesses of the approach that generally have to do with its applicability to actual fisheries situations. First, search theory applications assume random search behavior by fishermen and distributions of fish schools which have been verified only rarely by empirical data. The former assumption is the most questionable, as fishermen are known to direct their

effort to areas of high concentrations, particular species, and even particular age classes within species (e.g. Cook 1984).

Second, Shotton's (1973) pioneering work was limited because it stipulated the best solutions for a specific example and for a given set of model parameters. Other authors (e.g. Mangel and Clark 1983) have attempted to overcome this limitation, by using dynamic programming. This technique determines the optimal solution by searching over all "possible" (as determined by the authors) states (e.g. fish densities), actions (e.g. areas to fish) and time periods and by calculating the value (e.g. net seasonal revenue) of each combination. The problem with dynamic programming is that solutions require searching over a number of outcomes equal to the number of states \times number of actions \times number of time periods (see Walters 1986 for an introduction to dynamic programming). This computational limitation, known as the "curse of dimensionality", has resulted in studies that lack realism. For example, studies commonly assume: (1) schools of uniform size that are not depleted as the season progresses, (2) perfect information, and (3) homogeneity of vessels both in terms of catching power and their economic objectives. Furthermore, studies generally only consider a few alternative actions (e.g. two alternative areas). While some of these assumptions can be relaxed, studies have been limited to either qualitative or very small quantitative extensions (e.g. Mangel and Clark 1983). Since the curse of dimensionality largely results from the lack of accessibility to the very highest speed computers, the limitations imposed by the curse of dimensionality may be overcome in the future as technology progresses.

Simulation Models

The technique of simulation modeling is in widespread use in biology and resource management. Thus, it is not surprising that a few examinations of movement patterns have used simulation models to test assumptions about possible types of movement patterns and their implications for resource exploitation. Yet considering that fisheries in some parts of the world (e.g. North Sea, NW Atlantic) have been monitored and managed for nearly 70 years, it is a bit surprising that the first fisheries models to included fleet components appeared about fifteen years ago and there have only been a few such studies since.

One of the first studies to consider fleet components in a fishery model was Caddy's (1975) examination of the scallop fishery on George's Bank in the NW Atlantic. Caddy compared a spatial model simulating nonrandom recruitment and harvesting with the standard yield per recruit model of Beverton and Holt (1957). The fleet component of Caddy's model was based on the simple formula for allotting effort shown below.

$$f_{ij} = \frac{CPUE_{ij}}{CPUE_T} \times f_T \quad (1.4)$$

where f_{ij} is the effort allotted to subarea ij , $CPUE_{ij}$ is the catch per unit effort in subarea ij , $CPUE_T$ is the total catch per unit effort of all subareas, and f_T is the total effort in all subareas. Since the scheme of proportional effort allocation resulted in lower than observed effort in high effort areas, Caddy

modified equation 1.4 to account for the average historical effort and catch per effort distributions.

Caddy found overall yield declined more sharply as effort increased beyond the point of maximum sustained yield in the spatial model compared to the yield per recruit model and he suggested an increase in yield could be obtained if effort could be diverted away from heavily fished areas. The suggestion of management of effort on a subarea basis was very different from the more general catch quotas and season length limits commonly used for demersal species.

A few papers have modeled the annual numerical responses of fishing fleets as a predator-prey system with Lotka-Volterra equations. The basic form of the Lotka-Volterra equations are:

$$\frac{dx}{dt} = rx - sxy \quad (1.5)$$

$$\frac{dy}{dt} = sxy - my \quad (1.6)$$

where x and y are the numbers of prey and predators, r is the prey's intrinsic rate of increase, s is the rate of capture of prey per predator, and m is the mortality rate of predators. The different formulations for equation 1.6 which in the case of the fishery refer to the change in numbers of boats, are of particular interest.

Gatto et al. (1976) applied a discrete time version of such equations where equation 1.5 was replaced by the Ricker (1954)

stock-recruitment model and equation 1.6 was replaced by:

$$B_{t+1} = sB_t + i \frac{C_t}{B_t} \quad (1.7)$$

where B is the number of boats, C is the catch and s and i are survival and investment coefficients of the fleet. After examining the models equilibrium properties, the authors concluded that the model was too crude for practical, quantitative applications. The principal weaknesses of the model were the assumption that investment was a linear function of catch per boat in the same year, and a failure to take alternative fishing locations and species into account.

Allen and McGlade (1986) considered the Lotka-Volterra approach as an alternative to simple fishery models such as the surplus production model of Schaefer (1957). They argued that Lotka-Volterra models have not been applied to fisheries because of a basic reluctance of managers to treat fishermen as an active part of the system.

The first part of their study used Lotka-Volterra equations in a simulation model of the Nova Scotia haddock fishery. Their model for haddock was similar to equation 1.5, except they included 3 age classes. Their equation for change in boats was:

$$\frac{dY}{dt} = RY(1 - \frac{C}{LPE\$}) \quad (1.8)$$

where Y is the number of boats, R is the rate of response of effort to profitability, C is the revenue per boat needed to maintain effort, and LPE\$ is the total landed value of the 3 age classes per boat. The price also fluctuated depending on the catch relative to the available markets. Initial deterministic runs of the model resulted in damped oscillations in both the numbers of fish and

vessels with an equilibrium occurring after 70-80 years. Next they allowed the birth rate (equivalent to r in equation 1.5) to fluctuate randomly about a mean value. The result was irregular oscillations in boats and fish. The oscillations were amplified by the lagged response of effort to fish abundance.

The second part of the study considered a multispecies, multifleet spatial model of Nova Scotian trawl fisheries. The additional components of the model included : (1) catch was determined by a type II functional response of Holling (1965), and (2) allocation of effort to different zones based on their relative "attractivity". Attractivity was a function of the expected profit, the quality of information and the homogeneity of the fleet. This effort allocation scheme was similar to Caddy's proportion effort allocation with the additional component of information flow between fleets. Thus, in Allen and McGlade's model vessels played the dual role of catching fish and transmitting information to other vessels. This form of effort allocation allowed the authors to examine different strategies among fleets such as the stochastic - cartesian comparison (see Chapter 3). Allen and McGlade's efforts represent the most sophisticated attempt to include fleet components in fisheries models to date.

Hilborn and Walters (1987) presented some general guidelines for simulating stock and fleet dynamics in fisheries with spatial differences. Their model for fleet dynamics included a method of sequential effort allocation. This scheme involved four steps (see their Table 1; p. 1368):

1. Determine the proportion of effort to be allotted to each spatial area for exploratory fishing.
2. Allocate exploratory effort to determine initial catch rates.
3. Divide the remaining total effort into subunits to be allocated sequentially.

4. Allocate one subunit of effort to the area with the highest catch rate, update the abundance and catch rate in that area and allocate next effort subunit to the area with highest catch rate (and so on, repeating step 4).

Like Allen and McGlade (1986), they modeled catch as a type II functional response. The model was applied to six stocks of abalone exploited by divers off Australia. They showed how the relationship between catch rate and abundance can be distorted depending on assumptions about handling times and the relative biomasses of abalone in the different stocks.

Simulation modeling of movement dynamics has provided some valuable insights into the importance of incorporating the fleet responses in fisheries models. Perhaps the greatest strength of simulation models was stated best by Hilborn and Walters (1987; p. 1366):

"The development of simulations forces explicit statements of assumptions and hypotheses, and encourages explorations of alternative hypotheses."

This property makes simulation models very good teachers and tools for asking a variety of "what if" questions. Other strengths of simulation modeling include flexibility, general ease of construction, and the relatively short time lag between formulation of hypotheses and results compared to field studies.

The main weakness of the simulation approach is that the explicit statements and hypotheses must be written in the form of equations that are suitable for programming. Unfortunately, not all hypotheses are amenable to quantification and often even quantifiable hypotheses are difficult to model realistically.

For example, Allen and McGlade (1986) caution that Lotka-Volterra models assume fluctuations in abundances are caused by factors intrinsic to the model (e.g. abundance of fish fluctuates in response to fishing); external forces (e.g. the environment) are not supposed to influence the variables. In addition, information flow and differential goals among fishermen are difficult to model realistically, because they involve factors that are difficult to quantify. This inability to capture realism makes simulation models of little value in prediction; there is always something missing, some interaction unaccounted for, and/or some hypothesis not considered in all simulation models.

Empirical Studies

Various authors have examined the movement responses of vessels in particular fisheries. Peterman et al. 1979 found that weekly effort by Georgia Strait salmon trollers increased following increases in weekly catch per effort (an index of abundance). Hilborn and Ledbetter (1979) found a similar aggregation response in British Columbia salmon seiners, although responses varied between years and vessel mobility classes. Mobile seiners (vessels that fished more than one area) showed a nearly linear response of weekly effort to the landed value per effort in the previous week, while effort by stationary vessels had a saturating response to landed value per effort. Millington (1984) found a similar dichotomy between the responses of mobile and stationary salmon gillnetters. Millington also used landed value per effort as his index of abundance. The use of landed values assumes fishermen are sensitive to revenue rather than physical yield and may respond to differences in prices between species and/or seasonal price changes.

Hilborn and Ledbetter (1979) proposed some alternative hypotheses to explain the numerical responses of seiners to changes in relative benefit (measured as landed value/days fished) in various salmon fishing areas off the British Columbia coast. Millington subsequently tested these hypotheses with data from salmon gillnetters. The hypotheses are: (1) movement follows traditional patterns independent of recent fish abundance, (2) movement equalizes the gross dollar returns to effort (LPE\$) in alternative fishing areas, or (3) movement maintains relative LPE\$ in alternative areas. These hypotheses provide a description of movement patterns in fisheries, and my approach in examining numerical responses was to test these hypotheses with data from the British Columbia trawl fishery.

Chapter 2: Effort Allocation in the British Columbia Trawl Fleet

Introduction

Three alternative hypotheses were proposed by Hilborn and Ledbetter (1979) to explain fleetwide movement patterns of salmon seiners and were subsequently tested by Millington (1984) with data on salmon gillnetters. I tested these hypotheses with data from the trawl fleet for two reasons: (1) the hypotheses provide a good framework for examination of movement patterns in the trawl fleet; and (2) the application of these hypotheses to trawlers provides a comparison to previous work on two segments of the salmon fleet. Brief descriptions of the rationale for each hypothesis, the hypotheses (H) and their predictions (P) are provided below.

I. Traditional Patterns

The rationale for the traditional patterns hypothesis is that fishermen may specialize on a particular area or set of areas, learn the best times to fish in each location, and develop fixed movement patterns that are independent of short term changes in abundance.

H: The fleet moves according to historical patterns.

P: The proportion of effort allotted to each area should be constant.

II. Equalize LPE\$

The Equalize LPE\$ hypothesis assumes fishermen are profit motivated, and that vessels will move to areas with high LPE\$ (landed value of the catch per unit of fishing effort). Hypothesis II makes four additional assumptions:

1. All boats are equal
2. All areas have equal desirabilities and fishing costs

3. Movement costs between areas are zero
4. There is perfect information about the potential benefits in each area.

If these assumptions hold or are nearly correct, then vessel movement should result in nearly equal LPE\$ in all areas.

H: The fleet moves to equalize gross returns to effort (LPE\$) in all areas.

P: Each area's LPE\$ should approach the average LPE\$ for all areas.

III. Maintain Relative LPE\$

The Maintain Relative LPE\$ hypothesis was proposed for cases when assumption 2 above is violated. If areas have different desirabilities and costs, vessel movement should result in the LPE\$ in each area remaining constant relative to the average LPE\$ of all areas. Areas with consistently higher costs should have consistently higher LPE\$ and vice versa. Note that assumptions 1, 3, and 4 above also apply to the Maintain Relative LPE\$ hypothesis.

H: The fleet moves to maintain relative LPE\$'s in each area.

P: The ratio of each area's LPE\$ to the average for all areas should be constant.

The effects of violations of the assumptions of the Equalize LPE\$ hypothesis on the conclusions of this chapter are examined in chapter 3.

Data and Methods

Description of the Fishery

The B.C. trawl fishery provides a good test case for the Hilborn-Ledbetter hypotheses. Over the last twenty years the trawl fishery has averaged about 100 licensed vessels of which 60-80 actively fished in any given year (For a historical review of the development of the B.C. trawl fishery and trawl gear see Lippa 1967). The principal species landed by the trawl fleet include Pacific cod (*Gadus macrocephalus*), lingcod (*Ophiodon elongatus*), Pacific hake (*Merluccius productus*), walleye pollock (*Theragra chalcogramma*), various rockfishes (*Sebastes* spp.), flatfishes (Pleuronectid spp.), sablefish (*Anoplopoma fimbria*) and dogfish (*Squalus acanthias*). The total landings of all species have fluctuated around 30,000 metric tons in recent years (Leaman and Stanley 1987). The fishery is regulated by the Offshore Division of the Canadian Department of Fisheries and Oceans (DFO), and the primary method regulation has been catch quotas.

The fishery is highly structured in space with fishing occurring on a series of relatively discrete trawling grounds at particular depths and seasons for the various target species (Fig. 2.1). For example, during the summer months fishermen may choose between trawling for Pacific ocean perch (*Sebastes alutus*) in the deep waters (>100 fathoms) of Goose Island Gully (Area 5), Pacific cod and flatfish in the shallower waters (30-50 fathoms) on Two Peaks-Butterworth ground in Hecate Strait (area 6), lingcod on Big Bank (Area 1), or Pacific hake in area 3 (Fig. 2.1). The opportunities for movement are virtually unregulated with the exception that some areas may become less attractive when quotas for particular species in those areas have been caught.

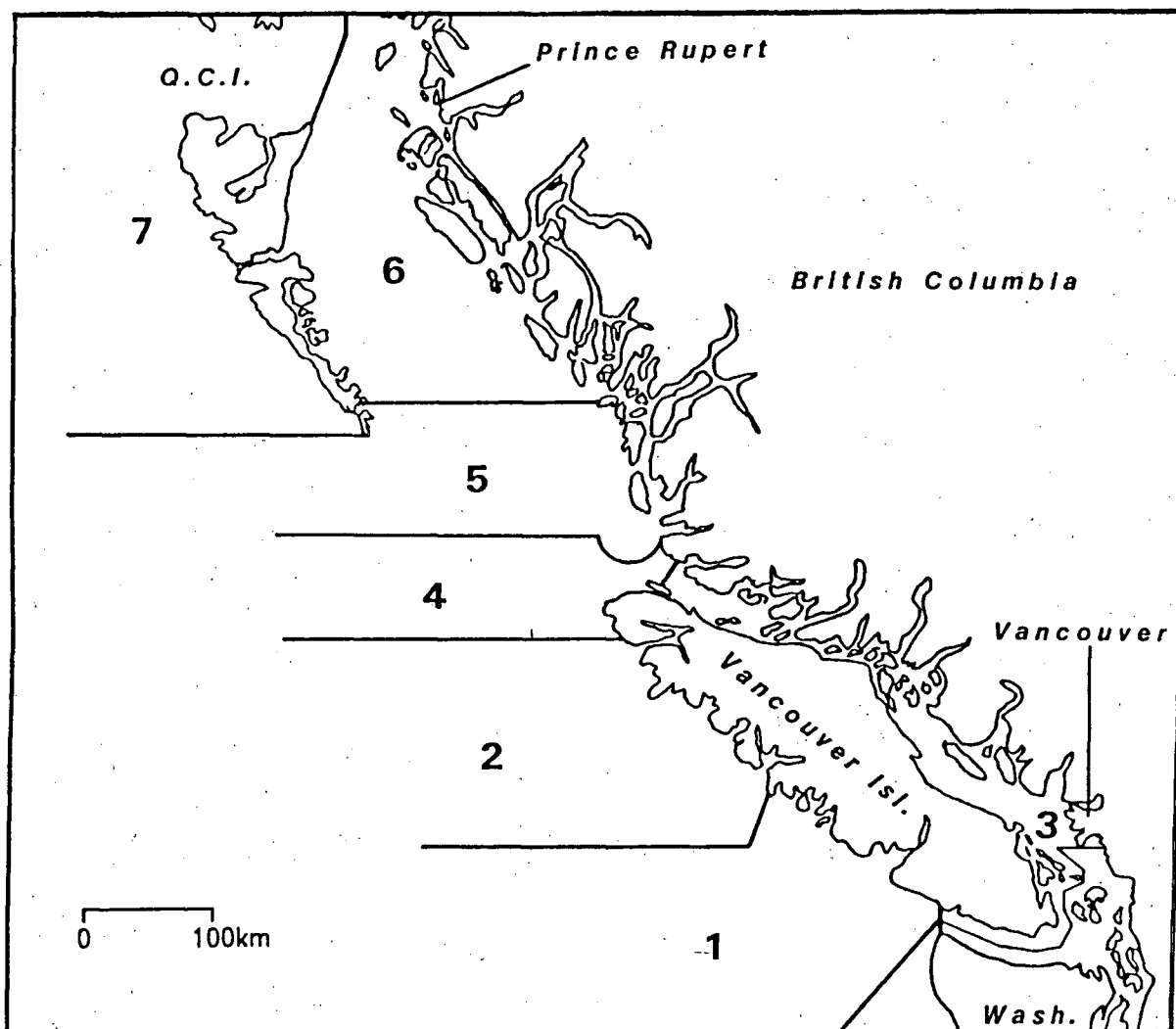


Figure 2.1. Map of seven areas chosen for analysis and two major landing ports for groundfish on Canada's Pacific coast.

Trawl gear consists of a large flattened funnel shaped net attached to the stern of boat by two cables (warps). During the towing process, the front of the net is forced open laterally by two rectangular otter boards that are attached to each warp. Floats attached to the top of the net opening and weights attached to the bottom open the net vertically. The net is usually towed along the sea

bottom and fish are forced down the funnel into the rear of the net (codend). The net is retrieved by a winch or pair of winches. There are many variations in the components of trawl gear, see Lippa (1967) for more detail.

Data Sources and Statistical Tests

The analysis is based on DFO saleslips and license data for the years 1967-1981 and 1967-80 respectively. A saleslip is recorded for each landing made by a vessel and includes the following information: landings (lbs.) and values (\$) of fish by species (or species group), the location of catch by statistical area, fishing effort (days fished), the company purchasing the fish, and the date landed. The license data are collected annually on vessel registration forms and include measurements of various vessel attributes such as length, tonnage, and horsepower as well as the location of home port, type of vessel ownership, and numbers of licenses held. Thirty-one DFO statistical areas were grouped into seven areas that include the major fishing grounds exploited by the trawl fleet.

The question of how effort is distributed among fishing areas can be posed at various spatial and temporal scales. In the analysis that follows, I will consider two temporal scales, between and within years, and the fixed spatial scale as determined by the seven areas.

The hypotheses predict how effort responds to changes in potential benefits, and therefore it is important to define the units of measurement for these two factors. The units for effort are *days fished*, and like Hilborn and Ledbetter (1979) and Millington (1984), I have chosen the *landed value(\$)/days fished* (LPE\$) as my measure of potential benefits. The choice of *dollars/days fished* assumes that profit is the primary motivation for fishermen. While the

measure has the advantage of lumping different species using the common currency of dollars, it ignores any possible species specialization that may be important to some fisheries in particular areas.

Hypotheses II & III predict patterns in the landed value/days fished between areas and across the fifteen years of the data base. A price index was needed to account for the affects of inflation over the period, because the prices of the various species landed in each area may have experienced different amounts of inflation. Although Statistics Canada publishes price indices for fish in British Columbia these indices are affected most by high valued species such as, salmon, herring, and halibut that are not landed by the trawl fleet. To eliminate the affects of these species, a price index for groundfish was calculated from the saleslip data.

The methods used to calculate price indices were as follows. I used the equations below to calculate (1) a price index (I_{sy}) for each species (s) and year (y) and (2) a total annual index (I_y).

$$I_{sy} = \frac{P_{sy} Q_{sb}}{P_{sb} Q_{sb}} \quad (2.1)$$

$$I_y = \frac{\sum_s P_{sy} Q_{sb}}{\sum_s P_{sb} Q_{sb}} \quad (2.2)$$

where P is the ex-vessel price/lb. in dollars, Q is the quantity landed (lbs.) and the subscript b denotes the base year. Note that equation 2.1, the standard equation for a price index, reduces to

$$I_{sy} = \frac{P_{sy}}{P_{sb}} \quad (2.3)$$

Each species index, I_{sy} , is the ratio of the price in the index year to the price in the base year. The annual index, I_y , is a weighted ratio of prices where the weighting factors are the quantities landed of each species in the base year. Following the procedure of Statistics Canada (1983), I selected the average of three years as my base period (1979-1981). I calculated a price index for 12 species or groups for each year using prices and landed values from the saleslip data for all areas and trawl vessels (Table 2.1).

I used the price indices in Table 2.1 and the equation below to correct landed values for inflation.

$$CLV_{ay} = \sum_s \frac{LV_{say}}{I_{sy}} \quad (2.4)$$

where CLV is the corrected landed value of the catch in dollars, LV is the total landed value of the catch, I is the price index, and the subscripts a , y and s denote the area, year, and species. I applied the species specific price index to account for possible variability in inflation effects between areas with different species.

I chose certain non-parametric methods (Spearman rank correlation, Kendall's concordance, and Kruskal-Wallis nonparametric ANOVA) for my statistical analyses.

Table 2.1. Ex-vessel price indices for selected trawl caught groundfish species or groups landed in British Columbia 1967-81. (1979-81 = 1).

Year	Species ¹												yind ²
	Pcod	lcod	sabl	rock	sole	flou	turb	poll	hake	skat	dogf	misc	
1967	30	23	32	33	28	52	19	32	0	68	36	21	27
1968	29	25	38	32	27	59	0	43	0	52	47	24	28
1969	31	27	39	37	24	37	0	87	0	40	67	24	30
1970	36	34	36	39	27	49	38	104	0	48	30	35	35
1971	38	38	33	38	30	48	0	0	0	47	30	38	32
1972	36	40	35	35	32	41	46	54	0	40	30	35	33
1973	42	54	35	43	45	61	66	59	0	54	60	44	42
1974	53	72	37	54	63	63	68	65	0	59	48	27	51
1975	53	45	38	55	58	65	67	74	0	62	43	53	51
1976	54	58	49	54	56	65	68	70	0	61	54	48	51
1977	67	80	64	65	65	81	67	71	0	60	71	74	64
1978	83	107	91	80	80	109	86	83	0	73	94	15	73
1979	99	129	93	101	102	93	91	99	0	85	100	69	92
1980	99	81	66	99	97	111	106	98	118	100	100	71	95
1981	100	93	116	99	100	103	104	105	98	107	96	107	101

¹ Species codes: Pcod = Pacific cod; lcod = ling cod; sabl = sablefish; rock includes Pacific ocean perch, & yellowmouth, greenstriped, yelloweyed & other rockfishes; sole includes petrale, butter, dover, english, rex, & rock soles; flou includes Pacific sanddab & starry flounder; turb = turbot; poll = walleye pollock; hake = Pacific hake; skat = skates; dogf = spiny dogfish; misc includes nonfood fish, octopus, halibut, squid, plankton, eulachons, sturgeon, perch, crab, & other fish.

² yind = annual index.

I used Spearman's rank correlation (Siegel 1956; p. 202) instead of product-moment correlation in most cases because of the highly variable nature of catch and effort data. The variability was particularly large on the weekly time scale (e.g. Fig. 2.11), and the use of rank correlations minimized the effect of outliers. Another advantage of using rank correlations was that the Kendall's concordance statistic (W; Siegel 1956; p. 229) provides a measure of the similarity of rankings among all years. Note that the use of product-moment correlations (i.e. in Tables 2.3a, b and 2.4, and Figs. 2.6, 2.8, and 2.9) would not have changed the qualitative results.

I performed Kruskal-Wallis nonparametric ANOVA's (Siegel 1956; p. 184: i.e. Tables 2.5, 2.6 and 3.1) rather than parametric ANOVAs because of the skewness and heteroskedasticity of the data. I was able to correct for the skewness by log transformation, but variances among treatments (i.e. areas or weeks) were significantly different (by an F test; Cooley and Lohnes 1971). Parametric one-way ANOVAs also showed significant differences, but the assumption of homogeneity of variance was violated. For further explanations of the specific tests mentioned above see Siegel (1956) and Zar (1974).

Description of Areas

Figure 2.1 shows the seven areas chosen for the analysis. They are: (1) Southwest Vancouver Island, (2) Northwest Vancouver Island, (3) Inside Vancouver Island, (4) South Queen Charlotte Sound, (5) North Queen Charlotte Sound, (6) Hecate Strait, and (7) West Queen Charlotte Islands. Each area includes a major fishing ground or aggregate of grounds exploited by the trawl fleet.

Also noted on the map are the two major ports for landing groundfish on the coast; Vancouver and Prince Rupert. These two ports accounted for 76-97% of the annual landed weight during the time period. Figure 2.2 shows the contribution of each of the seven areas to the weight landed and effort expended. Most of the effort has been exerted in areas 1, 3 and 6. Areas 1, 5 and 6 contributed most of the landed weight. The weight landed in Area 3 is small in comparison to the effort because area 3 is exploited by a large number of relatively small vessels (Fig. 2.2).

Results

Mobility in the Trawl Fleet

Previous studies of movement patterns (Hilborn & Ledbetter 1979, Millington, 1984) have indicated the importance of distinguishing between nonmobile or stationary vessels (i.e. vessels that fish only one area) and mobile vessels (i.e. vessels that fish two or more areas). This section briefly examines three aspects of mobility in the trawl fleet: (1) the ratio of mobile to stationary vessels, (2) the relative contribution of these vessels to the landed weight, values, and effort expended in each area, and (3) mobility differences between areas.

The ratio of mobile to nonmobile vessels in the trawl fleet (all years combined) was 1.3:1 (56%:44%). This ratio fluctuated annually from a minimum of 0.92:1 in 1974 to a maximum of 2.03:1 in 1980, but there was no time trend ($r^2=0.03$, $P<0.56$). More than half of the mobile vessels fished in three or more areas per year. Despite nearly equal numbers of mobile and stationary vessels, mobile vessels accounted for 88% of the landed weight and value and

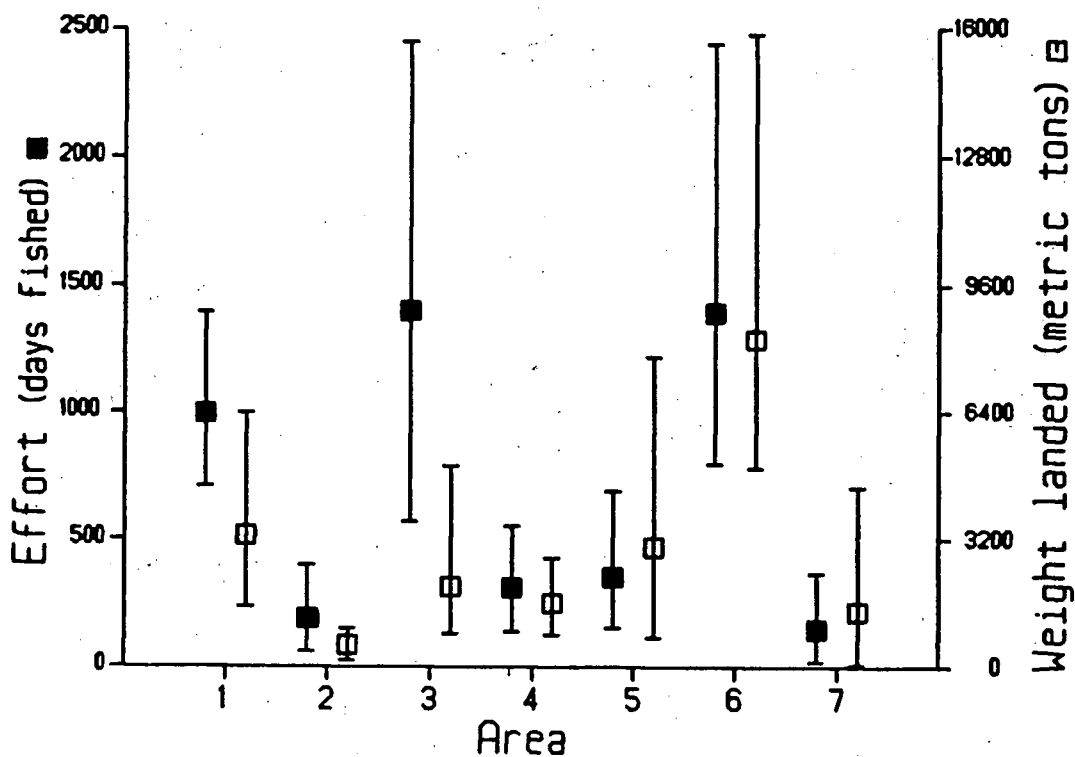


Figure 2.2. Contribution of the seven areas to weight landed (lbs.) and effort expended (days fished). Squares are means and error bars the range over the period 1967-81.

76% of the days fished (Table 2.2).

Stationary vessels were generally confined to areas with landing ports (i.e. areas 1,3,6). Sixty-six percent of all stationary vessels over the 15 years fished in area 3, while 18% and 12% fished in areas 6 and 1, respectively. But even in these areas, their contribution to landed weights, values and effort expended was rather small relative to mobile vessels with the exception that stationary vessels accounted for 49% of the effort expended in area 3 (Table 2.2).

The ratio of mobile to nonmobile vessels within each area also fluctuated annually, but there were no significant time trends in any of the areas. For the

Table 2.2. Summary of mobility statistics for the trawl fleet. Numbers are totals or percentages for the period 1967-81. The column "Mobil. class" is the number of areas fished per year (i.e. 1 = 1 area, 2 = 2 areas, 3+ = 3 or more areas). Each area column contains the totals or percentages for each category and mobility class (e.g. of the 645 vessels that fished area 1 over the fifteen year period, 223 fished 2 areas per year). The column "All areas" contains coastwide totals and percentages for each mobility class (e.g. 642 vessels fished only 1 area per year during the years 1967-81).

Category	Mobil. class	1	2	3	Area 4	5	6	7	All areas
No Vessel- years	1	80	9	422	5	5	117	4	642
	2	223	23	200	48	31	138	83	373
	3+	342	222	227	345	275	299	68	457
Tot Vessel- years		645	254	849	398	311	554	155	1472
% Vessel- years	1	12	4	50	1	2	21	3	44
	2	35	9	24	12	10	25	54	25
	3+	53	87	27	87	88	54	44	31
% Landed Weight	1	6	1	23	0	0	19	9	12
	2	35	3	44	10	11	38	43	31
	3+	59	95	33	89	88	43	48	57
% Landed Value	1	6	3	28	0	1	18	11	12
	2	36	3	44	10	11	38	44	31
	3+	58	94	28	90	88	44	46	56
% Effort	1	10	3	49	1	1	25	4	24
	2	38	7	32	10	12	37	51	31
	3+	52	90	19	89	87	38	45	45

three areas with significant numbers of stationary vessels, the proportion stationary was not correlated with LPE\$. The differences in the number of mobile and stationary vessels between areas will be evident in the movement patterns described in later sections.

Traditional Patterns

The traditional pattern hypothesis for between-year effort allocation predicts that the proportion of effort allotted to each area remain constant between years. Figure 2.3 shows the proportion of effort plotted vs year for each area. As noted above, areas close to landing ports (SW Vancouver Island, Inside Vancouver Island, and Hecate Strait) have the greatest proportion of effort. The other four areas rarely receive greater than one-tenth of the total effort in any one year. While there is considerable variability in proportions between years, particularly in high effort areas, the areas have maintained quite consistent rank (Kendall's concordance, $W=0.87$ ($P<0.001$)). A concordance of 1.0 would mean that each area's rank remained constant across all years. This tendency for some areas to have consistently higher effort than others is consistent with the prediction of the traditional patterns hypothesis, but it would also result if some areas are consistently more attractive because they have more fish than others (i.e. the Maintain LPE\$ hypothesis).

I also looked for traditional patterns of within-year effort allocation by examining plots of cumulative effort vs. week. If effort is distributed according to some historical pattern, then the amount of effort exerted in an area each week should be similar between years, and the cumulative effort plots for an area for different years should overlap each other. The analysis was divided into two time

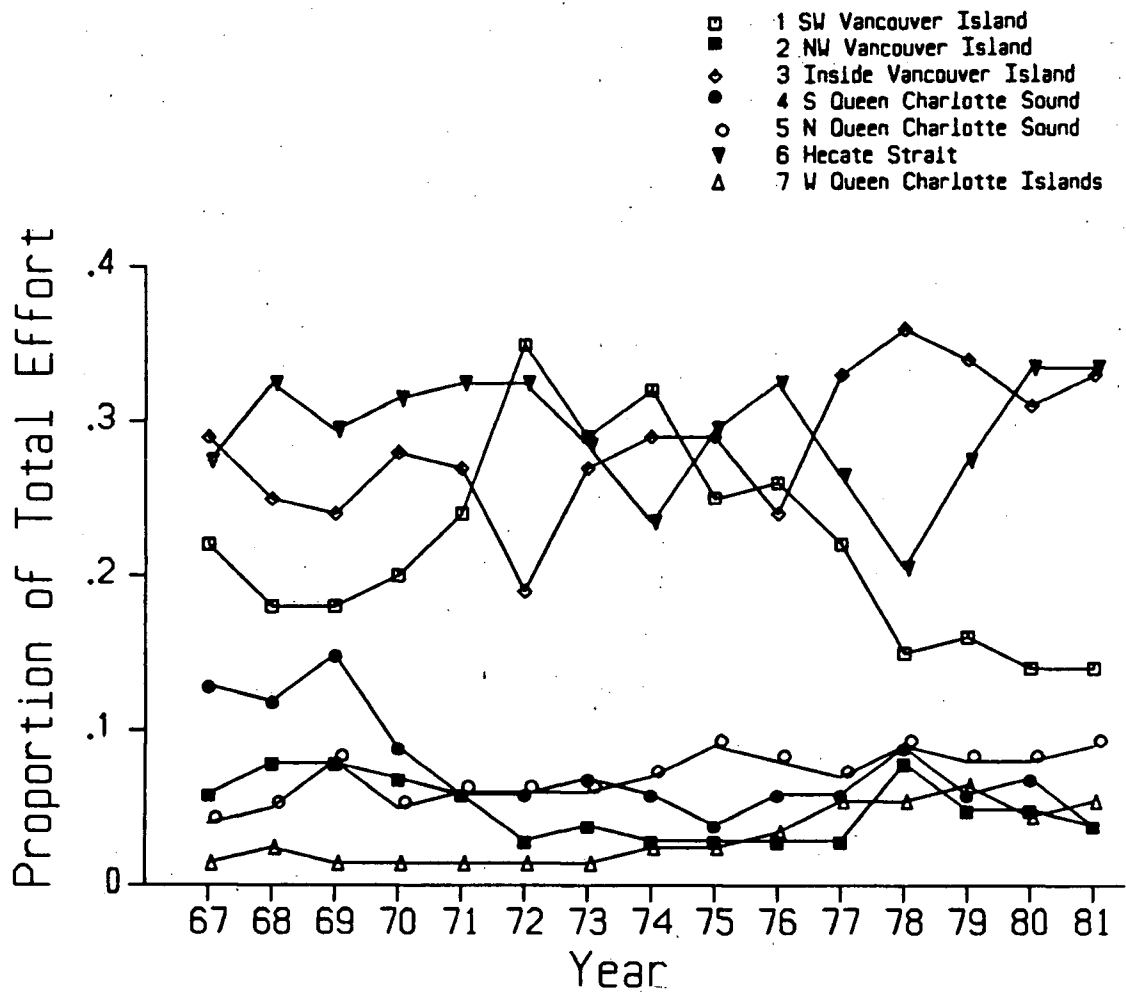


Figure 2.3. Proportion of the total annual effort allotted to each area in the years 1967-81.

periods, 1975-81 versus 1967-74, in order to detect long term changes in the predicted effort distributions.

Figure 2.4 shows the proportion of cumulative effort plots for the seven areas for the years 1975-81. The cumulative effort in each week is expressed as a proportion of the total effort in that area and year, to adjust for the fact that annual effort has increased in all areas over the time period and to permit

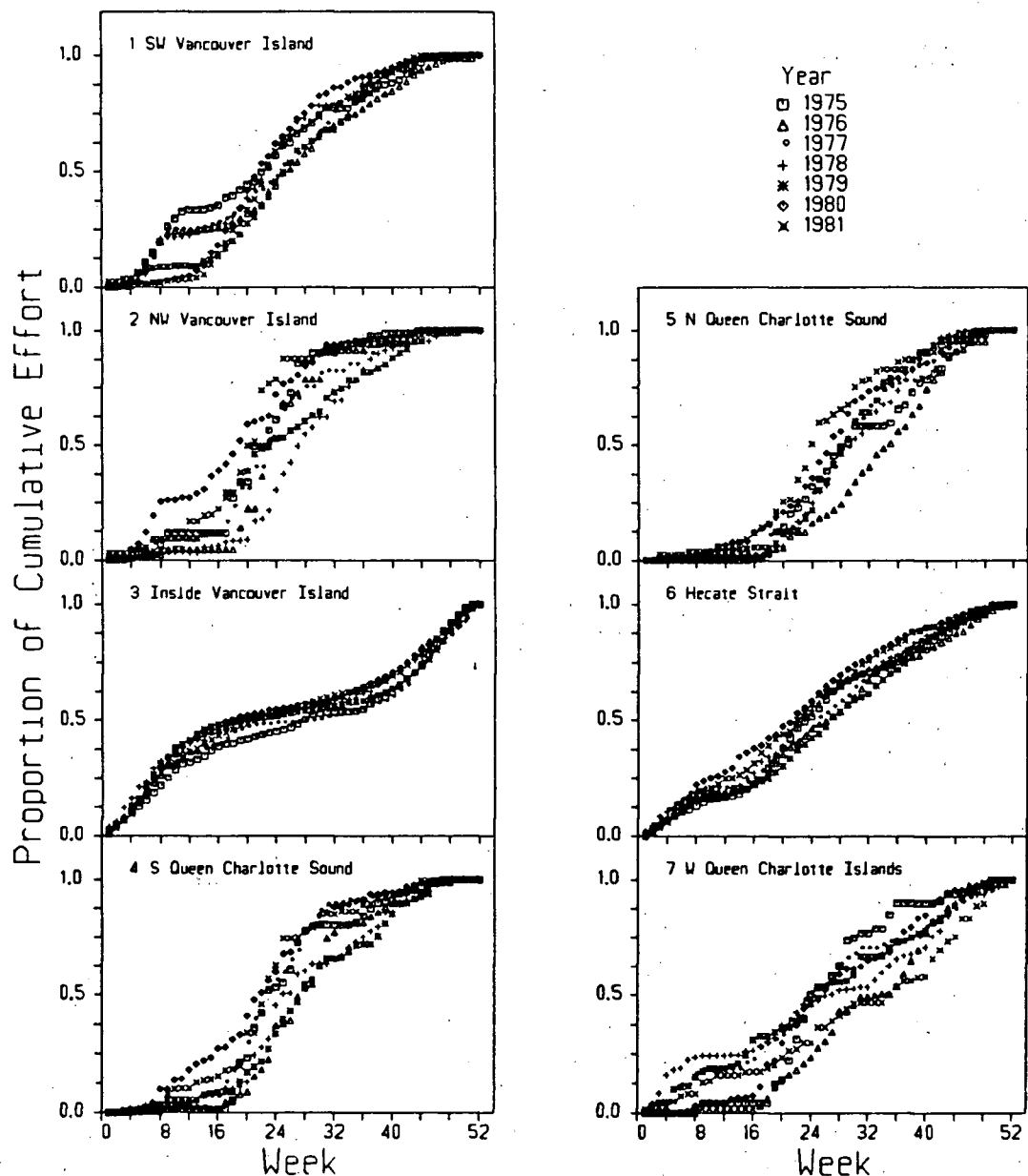


Figure 2.4. Proportion of cumulative weekly effort plots for the years 1975-81 in each area. The cumulative weekly effort is expressed as a proportion of the total effort in each area and year.

comparison of plots between years. Note the degree of overlap in areas 3 & 6 of the plots for different years. If the total annual effort in these areas could be predicted, a curve fit through the points would predict the weekly effort for

either area with reasonable precision. The cumulative effort plots for areas 3 and 6 are consistent with the predictions of the traditional patterns hypothesis.

The proportion of cumulative effort plots for Area 1 (SW Vancouver Island) and Area 7 (W Queen Charlotte Islands) show considerable scatter. These areas have been affected by regulations since 1978 that have closed certain grounds for short periods during each year (S.J. Westrheim, Pacific Biological Station, Nanaimo, B.C., pers. comm.). This effect is particularly evident in Area 1 where a closure to protect spawning cod has affected the timing of effort in the early part of each year (and apparently also the total effort as indicated in Fig. 2.3).

Areas 2, 4 and 5 are the farthest from ports of landing. All have a similar seasonal pattern in timing of effort with the major activity occurring during the middle part of the year, but each area shows considerable year to year variability in its effort pattern. The variability could be due to weather, as these areas along with area 7 are the most exposed areas on the the coast. Whatever the underlying cause, the effort distributions in these low effort areas located far from major landing ports, show much less overlap than areas 3 and 6, and are not consistent with the predictions of the traditional patterns hypothesis.

What is different about areas 3 and 6? Some differences have already been presented. Both areas are allotted large proportions of the total effort (Fig. 2.3), and each contain one of the two landing ports for groundfish (Fig. 2.1). Areas 3 and 6 also contain the largest proportion of stationary vessels (Table 2.2). These factors may have resulted in the overlapping relationships for areas 3 & 6, when compared to other areas. To examine long term changes in the

effort patterns I plotted the same curves for the earlier time period (1967-74) in the data base (Fig. 2.5).

For area 3, the main difference between years is the length of the winter fishery. For Area 6, the patterns between years are similar within the periods 72-74 and 68-71, but different between these periods. The primary difference between these two periods is an early season (weeks 8-16) drop in effort that only occurs in the latter period. The cumulative effort plots for area 1, the third area with significant numbers of stationary vessels, show more overlap during the period unaffected by the early season closure.

So far, I have just presented a graphical examination of the within-year traditional patterns hypothesis. To quantify the amount of overlap in the cumulative effort plots for each area over the entire time period (1967-81), I performed Spearman rank correlations on the weekly effort allotted to each area for each pair of years. Figure 2.6 shows Spearman rank correlations (r_s) plotted for consecutive pairs of years for each area. The Kendall's concordance values (W) for each area recorded on each plot are equivalent to an average rank correlation between all pairs of years. Area 3 had the highest consistency of within year effort pattern because of the large number of stationary vessels in area 3. Areas 4 and 5 have the next highest concordances, despite a predominance of mobile vessels. Area 6, that had overlapping plots for the 1975-81 period has a rather low consistency of rank for all years combined.

In conclusion, given the high concordance in rank of the proportion of effort allotted to each or areas over time, I cannot reject the traditional patterns hypothesis on the time scale of interannual variation. Within season patterns show much more variability between years, suggesting that traditional patterns

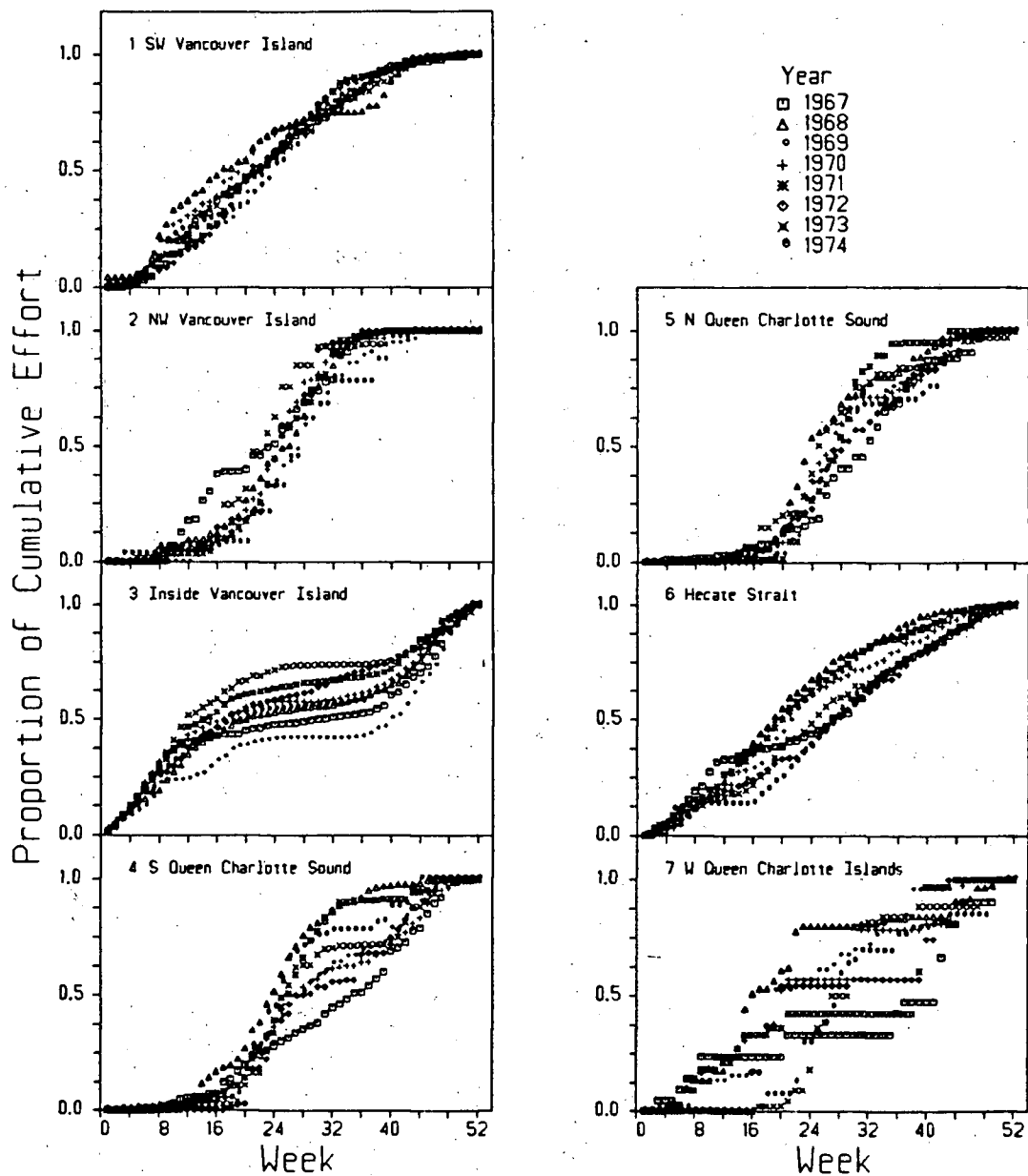


Figure 2.5. Proportion of cumulative weekly effort plots for the years 1967-74 in each area. The cumulative weekly effort is expressed as a proportion of the total effort in each area and year.

are modified by other factors. The next sections examine how temporal patterns in effort may be modified by numerical responses of effort to LPE\$.

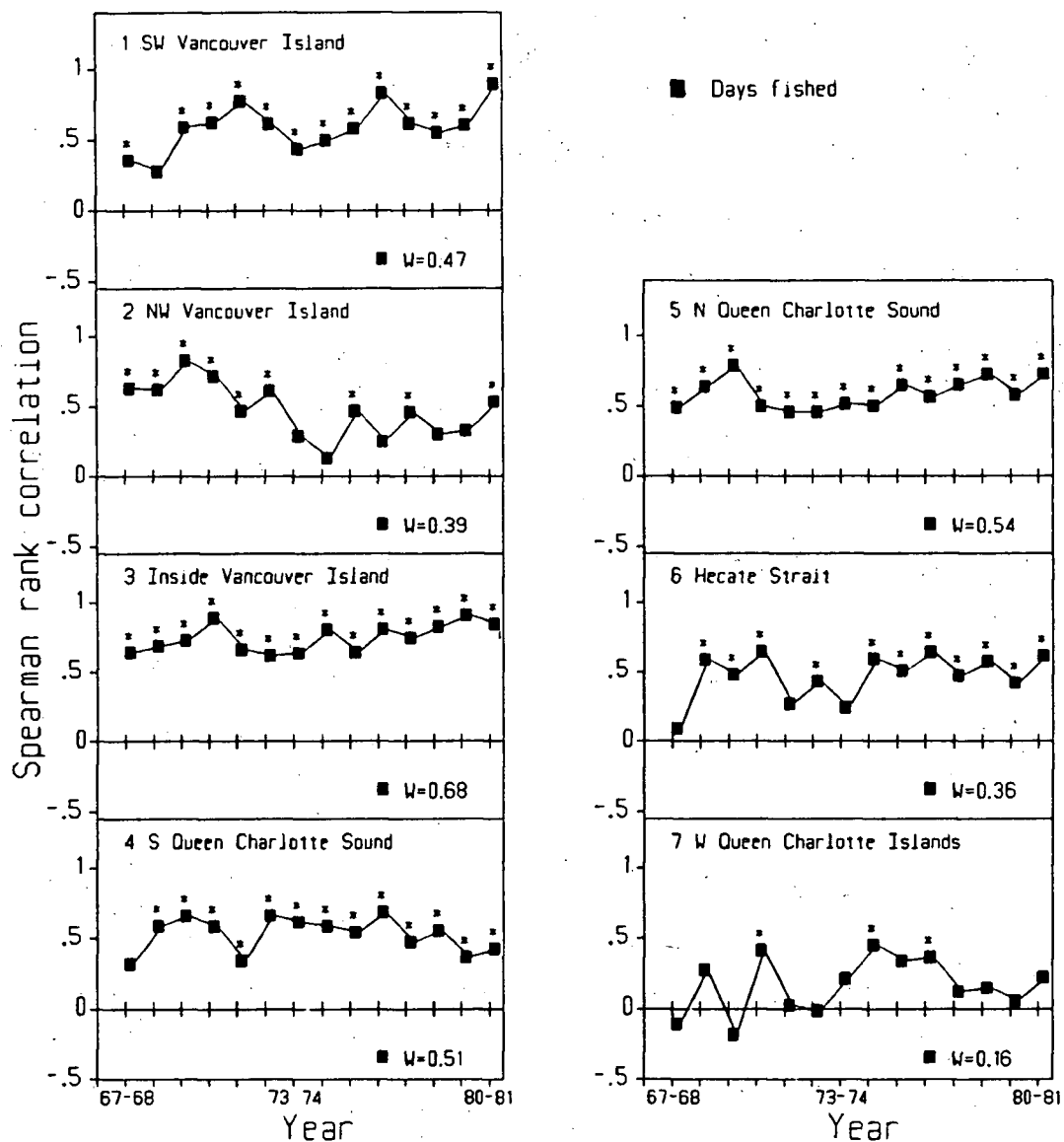


Figure 2.6. Spearman rank correlations (r_s) for weekly effort (days fished) and consecutive pairs of years 1967/68 - 80/81 in each area. Stars (*) indicate significance at $P < .05$. Kendall's Concordance (W) values are recorded on each plot. All concordances were significant at $P < .001$.

Hypotheses Using Landed Value Per Unit Effort

Assuming fishermen are profit motivated, I would expect the pattern of *landed value/effort* (LPE\$) to influence the choice of fishing location and affect the timing of effort in each area. Before numerical responses are explored in more detail, the next section examines a general problem with correlations between effort and LPE\$.

The Dilemma of Effort vs. LPE\$ Correlations

Although it is logical to expect increased benefits in an area to attract more effort to the same area (i.e. a positive numerical response), providing supporting evidence is difficult. The main problem is that covariation of effort and LPE\$ may be expressed in two different ways. When the measure of benefit is LPE\$, it may be impossible to separate the cause from the effect.

Two alternative explanations for covariation in effort are:

1. Increases in LPE\$ resulting from increased effort
2. Numerical responses of effort to increased LPE\$

Both these explanations must be examined to determine the cause of correlations between effort and LPE\$. For example, both effort and LPE\$ in Hecate Strait have the same seasonal pattern (Fig. 2.7), but it is not clear which factor is the cause and which is the effect.

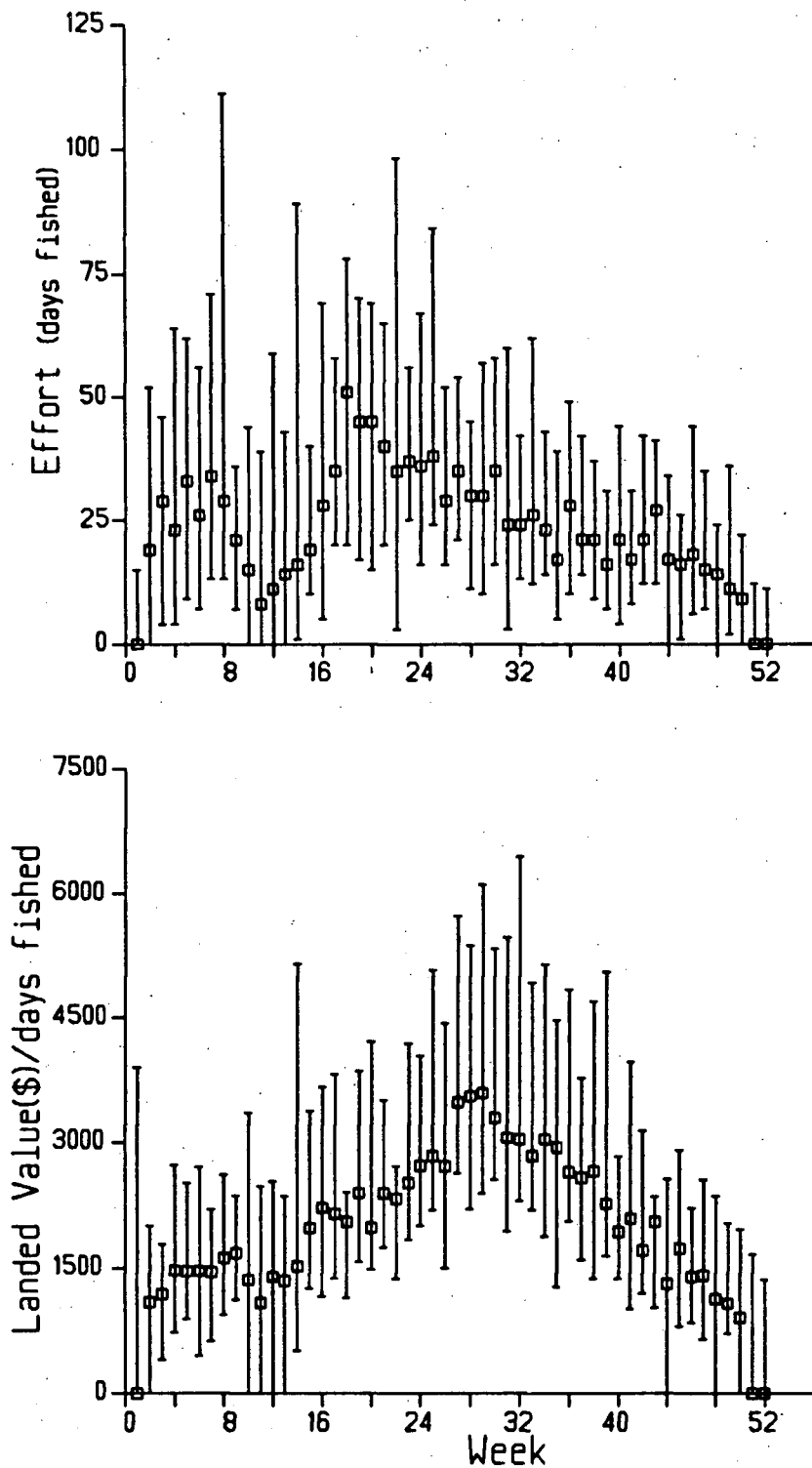


Figure 2.7. Effort and landed value(\$)/(days fished) vs. week for area 6, Hecate Strait. Squares are medians and error bars mark the interdecile range for the years 1967-81.

Increased effort could produce increased LPE\$ in two ways; either directly through learning and increased efficiency or indirectly through facilitation (e.g. using the positions of other vessels as an aid in locating fish). Therefore, explanation 1 may be restated as two questions:

1a. Is individual vessel LPE\$ increased when vessels fish more days?
(a learning response)

1b. Is vessel LPE\$ increased when more vessels fish in the same area?
(a facilitation response)

To examine question 1a, I calculated Spearman rank correlations, r_s , between days fished per trip and LPE\$ for all trips made to each area in the years 1967-81 (Table 2.3a). The coefficients are broken by vessel horsepower class to account for any possible confounding affects of vessel size (i.e. larger vessels fish more days and have higher LPE\$ than smaller vessels). Half of the correlations are not significant at $P < 0.05$. Thirty-one of possible 70 horsepower class-area combinations show significant positive correlations indicating LPE\$ increases as the number of days fished per trip increases. These correlations suggest that longer trips are associated with increased efficiency perhaps due to some within-trip learning by the skipper and crew. However, most of the significant positive correlations are for the smaller horsepower classes (i.e. 1-4) and these positive correlations may be an artifact of the effort measure. Many of the smaller vessels make short trips of 1-4 days. The actual number of hours trawled on a one day trip is less than the hours trawled on the second and third days of longer trips due to time spent steaming to and from port. Therefore, effort measured as days fished overestimates actual trawling time for one day trips relative to longer trips. Thus, LPE\$ is underestimated for the day trips relative to the longer trips, and that would result in the positive

Table 2.3a. Spearman rank correlations (r_s) between LPE\$ and days fished for ten vessel horsepower classes and seven areas. Numbers in parentheses indicate horsepower range included in each class. All years have been pooled. Correlations significant at $P < 0.05$ are in bold type. Two dashes (--) indicate too few observations to calculate correlation coefficient.

Horsepower class	1	2	3	Area 4	5	6	7
1(0-99)	.42	.86	.06	.20	-.08	.39	-.17
2(100-199)	.34	.28	.21	.21	.48	-.07	-.27
3(200-299)	.35	.24	.04	.25	.51	-.17	.39
4(300-399)	.18	.37	.22	.28	.30	-.16	.21
5(400-499)	.51	-.09	.08	.19	.19	-.02	-.04
6(500-599)	.05	.62	-.12	.40	.19	-.11	.29
7(600-699)	.19	.27	.47	.13	.08	.17	.14
8(700-799)	.20	-.01	-.02	.20	.19	.13	.01
9(800-899)	.09	.24	-.22	.20	.32	.04	-.79
10(>899)	.57	.16	--	.12	-.01	1.0	--

Table 2.3b. Spearman rank correlations (r_s) between LPE\$ and days fished for ten vessel horsepower classes and seven areas. As in Table 2.3a except trips with 1 days fished were excluded from the analysis.

Horsepower class	1	2	3	Area 4	5	6	7
1(0-99)	.39	--	-.12	.09	-.22	-.05	-.23
2(100-199)	.13	.12	.06	-.14	.24	-.21	-.32
3(200-299)	.27	.27	-.05	.02	.16	-.27	.10
4(300-399)	.14	.38	.09	.02	-.04	-.24	.14
5(400-499)	.38	-.07	-.16	.15	-.08	-.20	-.32
6(500-599)	.04	-.20	-.47	.16	.12	-.19	.01
7(600-699)	.01	.35	.35	-.01	-.05	.01	-.22
8(700-799)	.13	.04	-.04	.26	.08	.01	-.25
9(800-899)	.03	.21	-.15	.17	.32	-.07	-.86
10(>899)	.35	-.52	--	-.23	.22	1.0	--

correlations shown in Table 2.3a. To investigate the possible impact of this bias on my results, I recalculated the correlations excluding the 1 day trips (Table 2.3b). The reduction in the number of significant positive correlations by more than two thirds (from 31 to 10) indicates that the apparent increased efficiency of longer trips was probably an artifact of the effort measure.

Negative correlations in either table may be due to the fact that boats with high LPE\$ will fill their holds quicker and make shorter trips than vessels with lower LPE\$. Furthermore, LPE\$ values for various trip lengths (days fished) may not represent a random sample of skippers. More successful skippers are probably overrepresented in the shorter trips with higher LPE\$ and vice versa. I was unable to test for a skipper effect because data on the skipper were not collected and recorded for the 1967-81 time period.

Evidence against facilitation effects is shown in Table 2.4. Individual vessel LPE\$ does not increase with increases in the number of vessels fishing in area. In fact, 6 of 10 horsepower classes show significant negative correlations, perhaps due to competition for preferred trawling sites. Correlations for landed weight per days fished (LPEW) show the same pattern. Therefore, the negative correlations for LPE\$ are not due to increased supplies of fish depressing prices. The lack of a local supply effect on prices is not surprising, because most of the groundfish landed in British Columbia are exported and price is not determined by auction.

I have refuted two possible explanations for positive correlations between effort and LPE\$ (learning and facilitation) that might be confused with evidence of numerical responses to perceived abundance/price changes. The next section examines the numerical responses of effort to LPE\$.

Table 2.4. Spearman rank correlations (r_s) between individual vessel LPE and number of trips made by all vessels to the same areas during the same week for ten horsepower classes. Correlations are presented for both landed value per effort (LPE\$) and landed weight per effort (LPEW). All areas and years have been pooled.

Horsepower class	n	LPE\$		LPEW	
		r_s	$P(r_s \rho_s=0)$	r_s	$P(r_s \rho_s=0)$
1	962	-0.10	0.002	-0.17	0.0001
2	5434	-0.34	0.0001	-0.27	0.0001
3	4655	-0.18	0.0001	-0.13	0.0001
4	2968	-0.12	0.0001	-0.10	0.0001
5	943	-0.02	0.56	-0.06	0.08
6	749	0.01	0.78	0.01	0.77
7	641	-0.08	0.03	-0.09	0.03
8	910	-0.04	0.25	-0.04	0.17
9	422	0.16	0.001	0.13	0.007
10	61	-0.20	0.15	-0.20	0.13

Numerical Responses of Effort to LPE\$

If the timing of LPE\$ is affecting the timing of effort I would expect weekly effort patterns to be more predictable between years when the weekly LPE\$ are more predictable and vice versa. Figure 2.8 shows the r_s for effort from Figure 2.6 plotted with the r_s for weekly LPE\$ plotted for consecutive pairs of years for each area. The r_s values for effort and LPE\$ follow the same yearly trend in most areas with two notable exceptions. Area 3, Inside Vancouver Island, has a very predictable effort pattern but poorly predictable LPE\$ pattern. The large number of small stationary vessels that fish in area 3

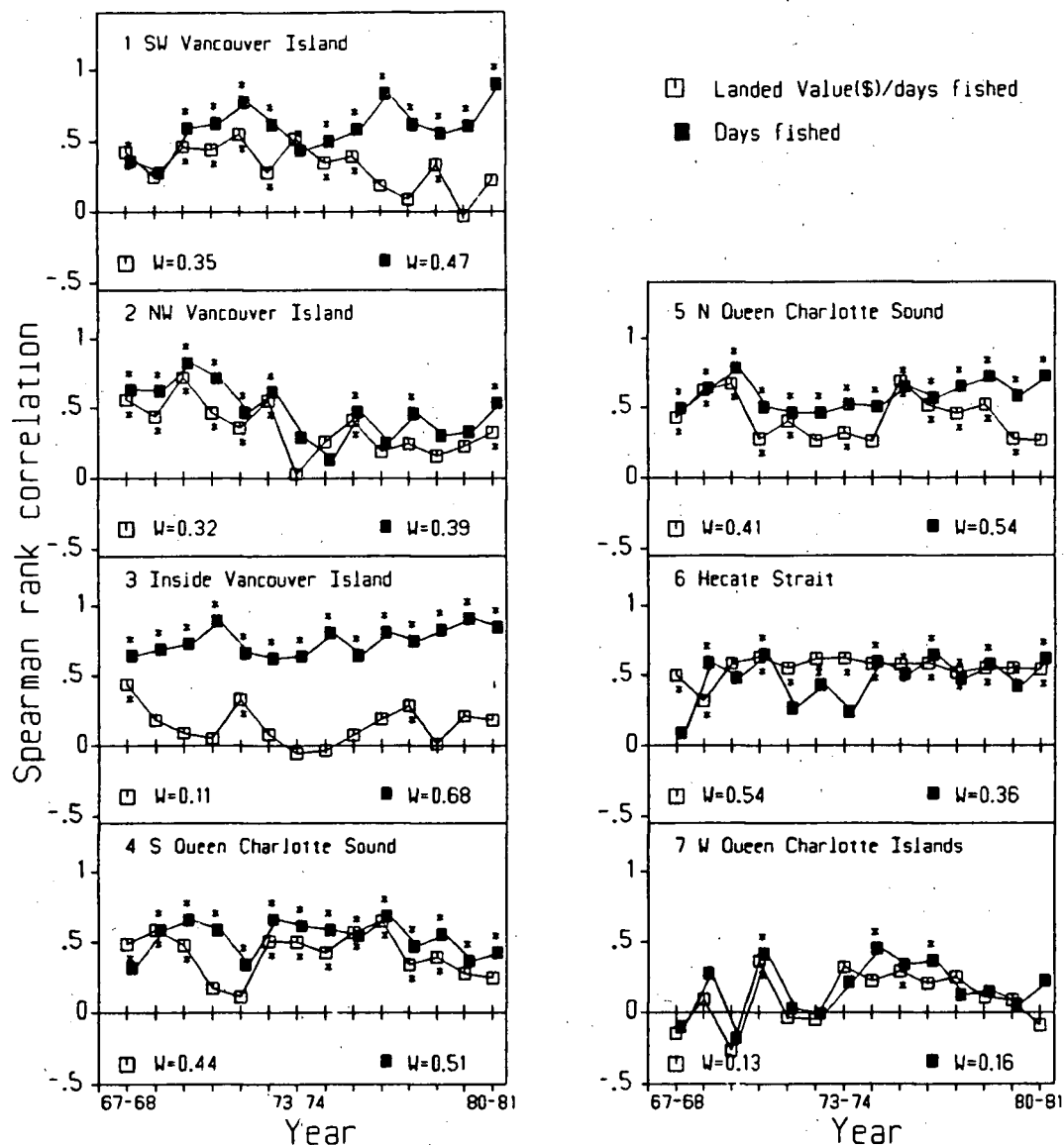


Figure 2.8. Spearman rank correlations (r_s) for weekly effort and landed value(\$)/(daysfished) in consecutive pairs of years 1967/68 - 80/81 in each area. Stars (*) above solid squares and below open squares indicate significance at $P < .05$. Kendall's Concordance (W) values are recorded on each plot. Concordances are significant at $P < .001$, and $P < .0001$ for weekly effort and landed value(\$)/(days fished) respectively.

are apparently willing to accept unpredictable LPE\$ in exchange for a more regular pattern of effort. The correlations for area 1, SW Vancouver Island,

follow the same trend for part of the time period, but the LPE\$ pattern is less predictable in the later years.

The close correspondence between effort and LPE\$ correlations depicted in Figure 2.8 could be due to a numerical response. If so, I would expect higher effort in an area to follow weeks with high LPE\$. Figure 2.9 is a plot of the r_s values for the numerical response of effort one week after the LPE\$. The majority of correlations are positive indicating that effort increases following weeks with high LPE\$. Areas with the most consistent pattern of LPE\$ also show consistent numerical responses between years. Areas 4 and 5 have the most consistent numerical response (highest concordance). These two areas are located farthest from the major landing ports where the cost of steaming to and from port, is greatest. The larger steaming costs increase the importance of fishing these two areas only when LPE\$ is high enough to offset costs.

I examined the data for evidence of interannual numerical responses, and found mixed results. Regressions of effort in year $(i+1)$ vs. LPE\$ in year i had significant positive slopes for areas 3, 5 and 7, but slopes were not significantly different from zero in the remaining areas (Fig. 2.10). The positive annual numerical response for area 3 is interesting considering the lack of a intra-annual response (Fig. 2.9). However, the positive relationships for areas 3, 5, and 7 should be interpreted with caution because there were significant positive time trends in both variates in each of these areas. Regressions of residuals from these time trends were not significant for any of the areas.

Correlations were found between intra-annual effort and LPE\$ patterns, associated with a positive numerical response particularly in two of the seven areas. I also found interannual numerical responses in three of the seven

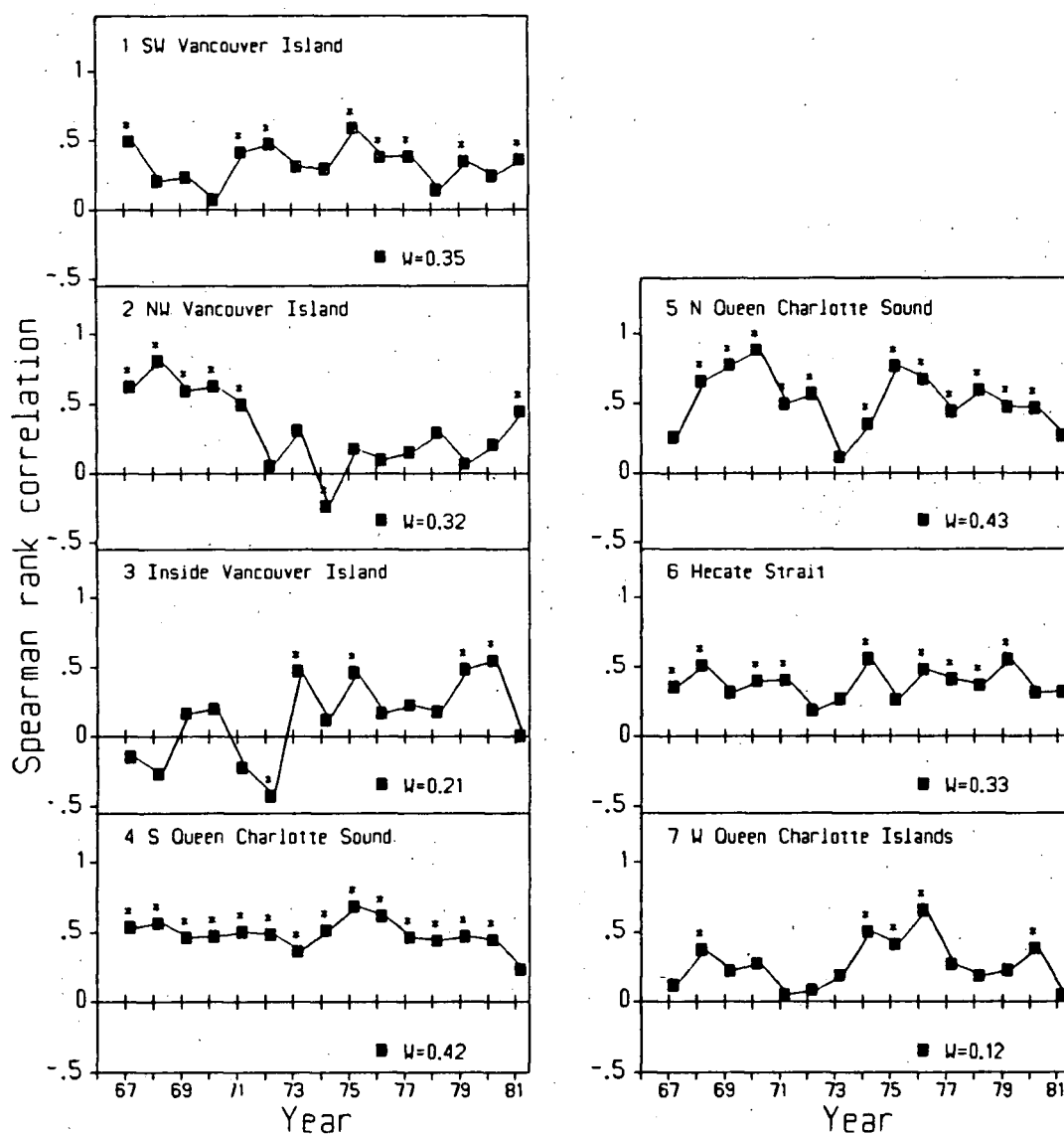


Figure 2.9. Spearman rank correlations (r_s) for the numerical response of effort (days fished) one week following landed values(\$)/(days fished) for the years 1967-81 in each area. Stars (*) indicate significance at $P < .05$. Kendall's Concordance (W) values are recorded on each plot. All concordances are significant at $P < .0001$.

areas, although the evidence is confounded by time trends in effort and LPE\$. The next two sections inspect these patterns in relation to the two remaining hypotheses that involve responses to LPE\$.

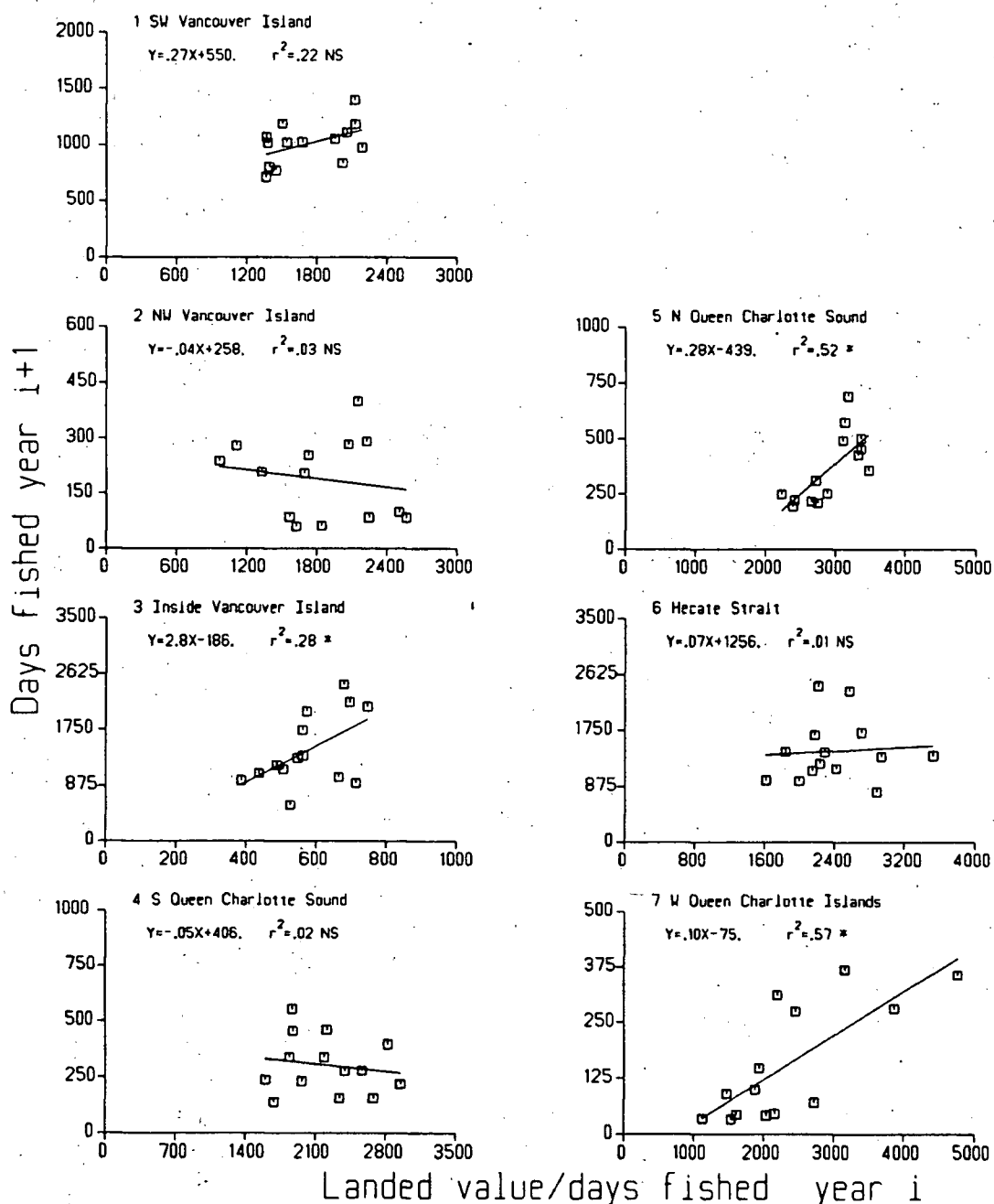


Figure 2.10. Effort (days fished) in year $i+1$ vs. landed value(\$)/(days fished) in year i with regression lines and equations for each area. NS, * indicate regression slopes not significantly or significantly ($P < .05$) different than zero, respectively.

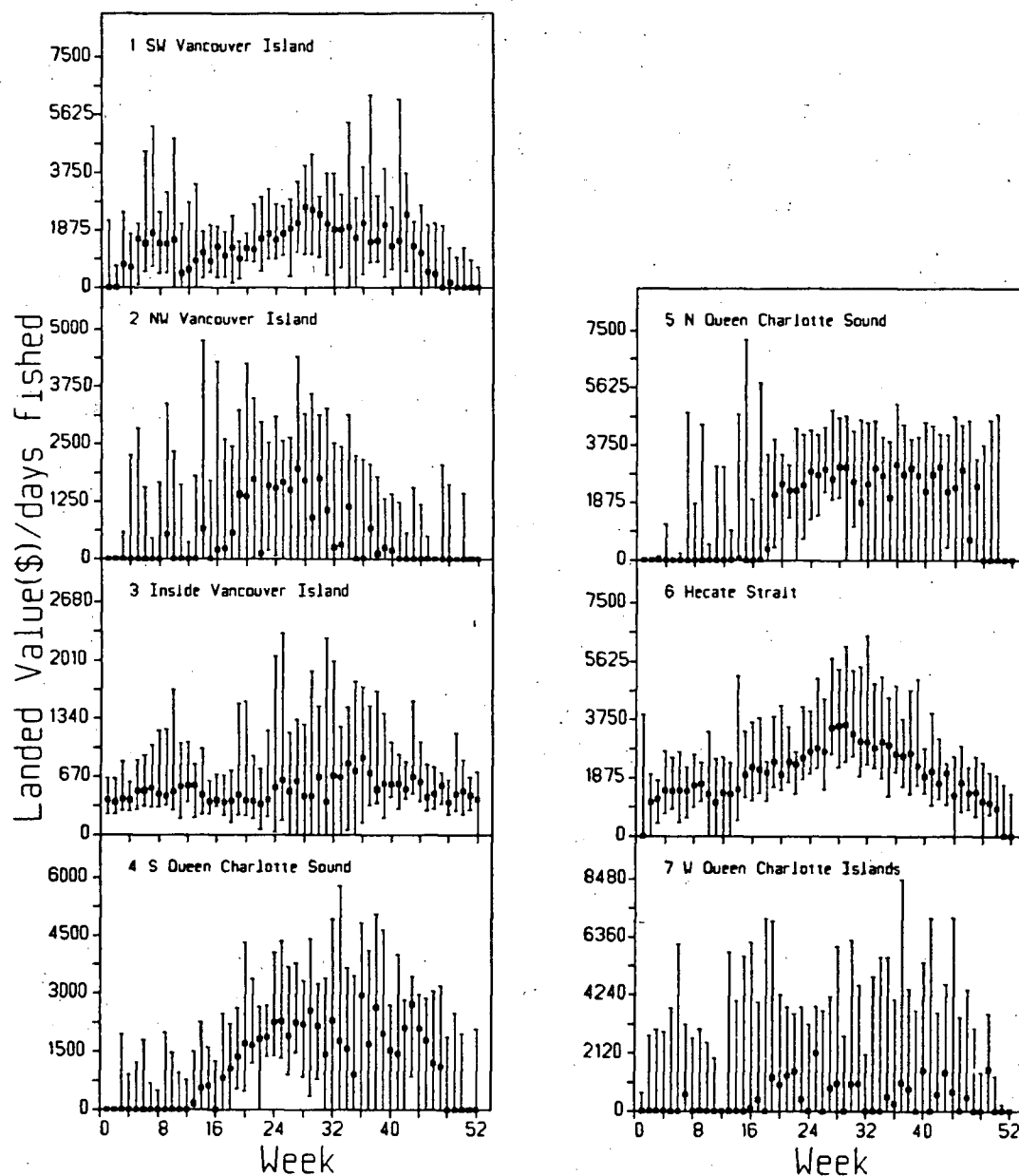


Figure 2.11. Landed value(\$)/(days fished) vs. week for each area. Squares are medians and error bars the interdecile range for the years 1967-81.

Equalize LPE\$

The Equalize LPE\$ hypothesis predicts that boats move to make the LPE\$ in each area tend toward the average LPE\$ of all areas. The within-year LPE\$

Table 2.5. Kruskal-Wallis nonparametric ANOVA comparing weekly LPE\$ in the seven aggregate areas. All years (1967-81) have been pooled. H_0 : The areas have the same weekly LPE\$s.

Area	n	avg.rank
1	780	3088
2	780	2032
3	780	2386
4	780	2694
5	780	2828
6	780	3799
7	780	2286
Total n	5460	

Kruskal-Wallis H Statistic = 654.1, df=6, $P < 0.0001$

patterns are shown in Figure 2.11. There are significant differences in weekly LPE\$ between areas (Table 2.5) indicating that vessel movement has not resulted in equal LPE\$ for all areas. Figure 2.12 plots the interannual LPE\$ pattern for each area. The concordance in rank ($W=0.67; P < 0.0001$) indicates areas have not tended toward the same average LPE\$. These tests clearly reject the hypothesis that vessel movements have equalized LPE\$ in the seven areas on either a within or between season time scale.

Maintain Relative LPE\$

A reinspection of Figures 2.11 and 2.12 shows that while each area does not tend towards the same average, some areas have consistently higher LPE\$ than others. This observation is confirmed by the concordance measure for

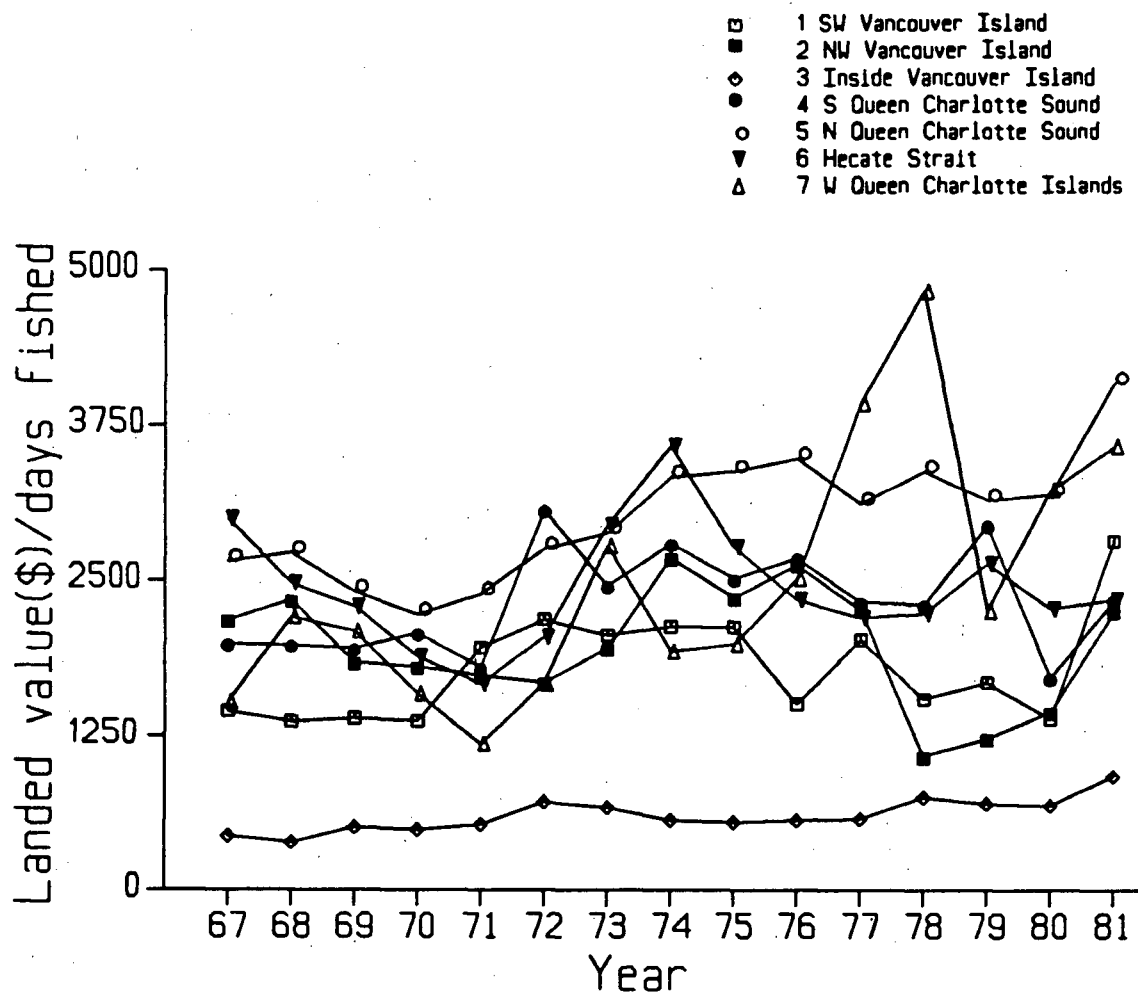


Figure 2.12. Landed value(\$)/(days fished) vs. year for each area in the years 1967-81.

between year LPE\$. If each area has its own unique time invariant desirabilities and costs, then vessel movement should maintain each areas relative LPE\$. The weekly ratios of each area's LPE\$ to provincial average LPE\$ (RPA) are plotted in Figure 2.13. There are significant differences between weekly RPAs within 5 of the 7 areas indicating that the weekly RPAs are have not remained constant within years (Table 2.6). The RPAs in Area 5 show marginally significant differences. The lack of significant differences in area 7 is probably due to the

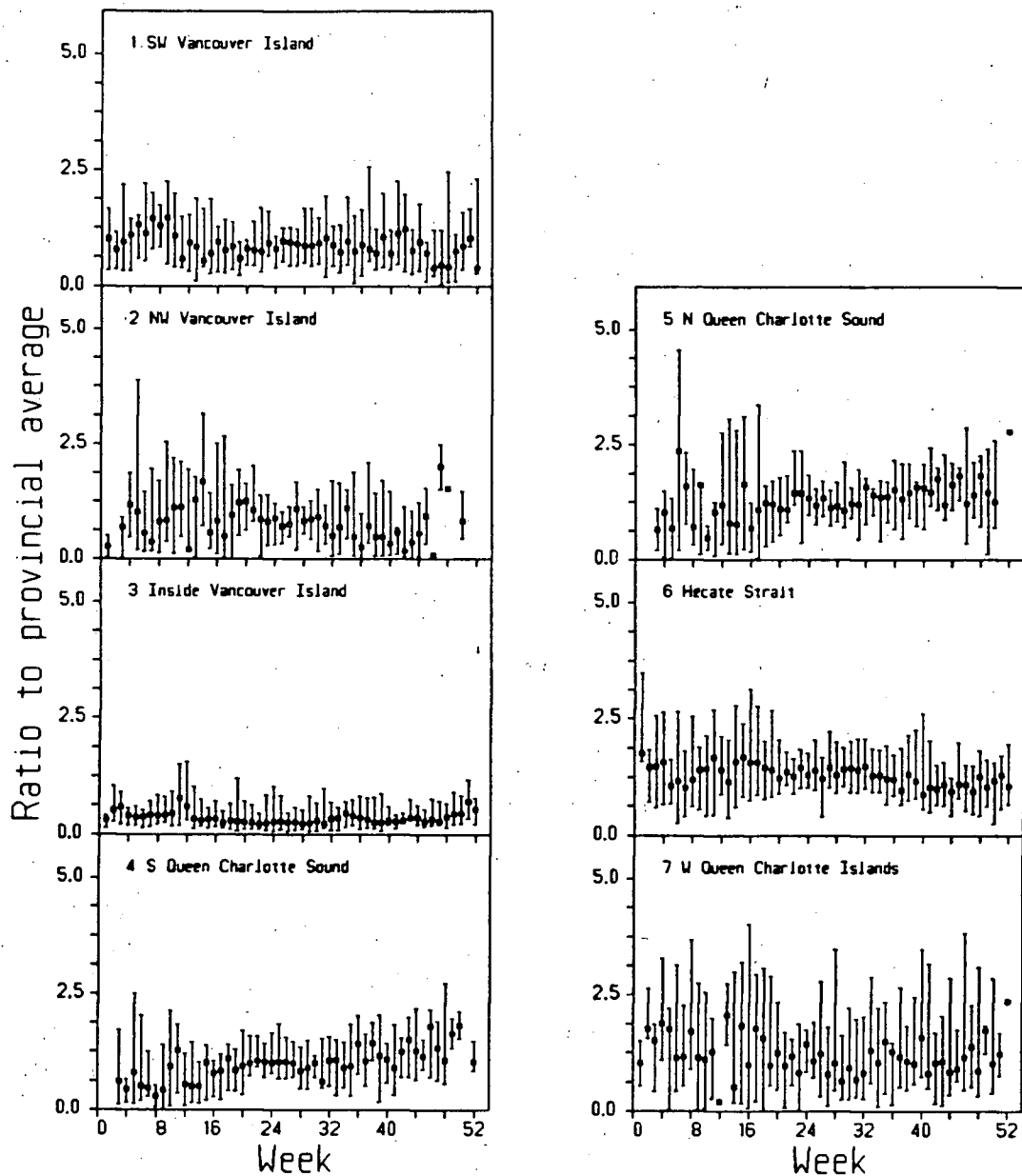


Figure 2.13. Weekly ratio to provincial average vs. week for each area. Squares are medians and error bars the interdecile range for the year 1967-81. Latter weeks lack rpa values or error bars because effort was either not present or present for only a few years.

large variability in weekly RPA for this area (Fig. 2.13).

Table 2.6. Summary of Kruskal-Wallis nonparametric ANOVAs comparing RPAs between weeks within each of the seven aggregate areas. All years (1967-81) have been pooled. H_0 : The weeks have the same RPA.

Area	H statistic	df	P
1	83.7	51	0.003
2	72.5	47	0.010
3	103.2	51	0.0001
4	111.4	48	0.0001
5	61.3	48	0.094
6	91.3	51	0.0006
7	41.8	51	0.82

Figure 2.14 shows the annual ratio to provincial average plotted for each area. The concordance ($W=0.67; P<0.0001$) indicates the annual RPAs have been fairly constant in rank among years.

Summary

This chapter examined the allocation of fishing effort by the trawl fleet to seven aggregate fishing areas located off the British Columbia coast. Three hypotheses proposed by Hilborn and Ledbetter(1979) were tested: I. Movement follows traditional patterns, II. Movement equalizes the gross dollar returns to effort (LPE\$) among areas, and III. Movement maintains relative LPE\$ in each area.

The major conclusions of this chapter are :

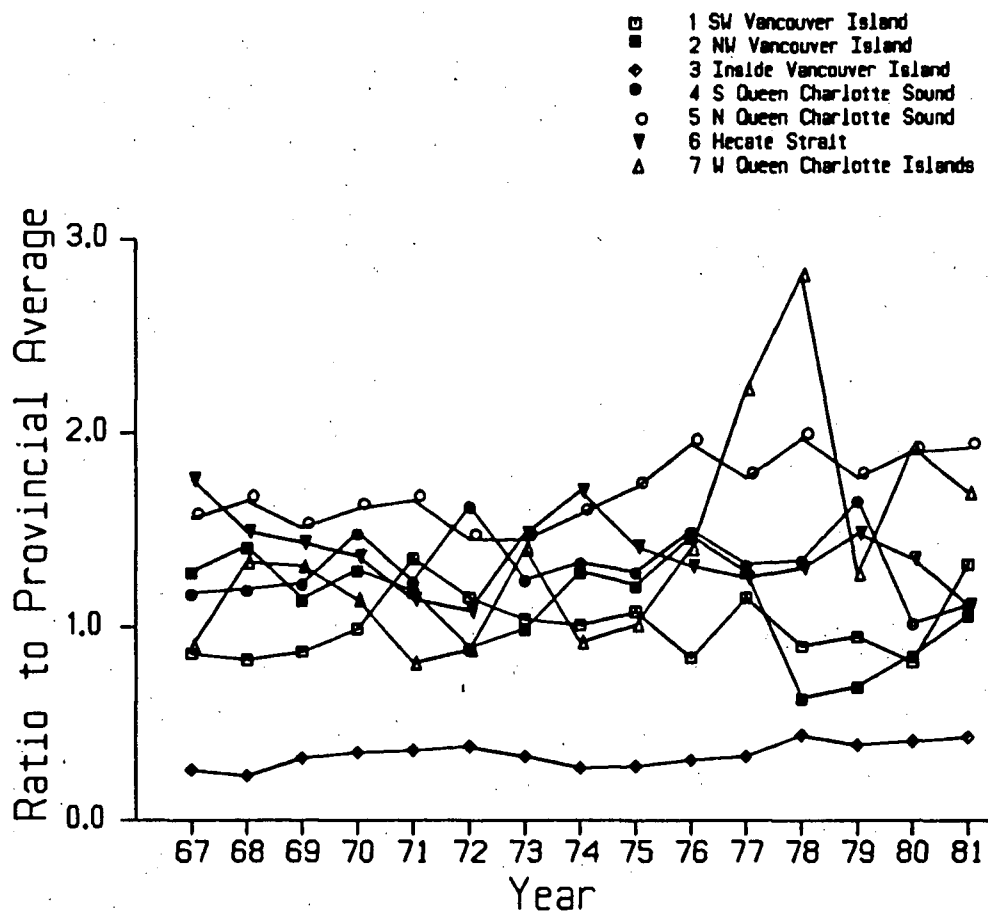


Figure 2.14. Ratio to provincial average vs. year for each area and the years 1967-81.

1. The proportion of effort allotted to each of seven aggregate areas maintains concordance in rank among years which is consistent with the traditional patterns and maintain relative LPE\$ hypotheses.
2. There is a traditional component to the within-year timing of effort, but effort timing is modified by changes in the timing of LPE\$ in all areas and by regulation in two of the seven areas studied.
3. Vessel movement has not equalized the LPE\$ in the areas.
4. The ratios of each areas LPE\$ to the average LPE\$ of all areas have not remained constant but do show concordance in rank across years which is consistent with the maintain relative LPE\$ hypothesis.

None of the hypotheses examined explain the observed within-year pattern of effort allocation. However two hypotheses, Traditional patterns and Maintain Relative LPE\$, are consistent with the among-year pattern. The latter hypothesis, however, still has some problems. Relative LPE\$s may be maintained by movement patterns, but also could result from differences in vessel size between areas. Furthermore, the rejection of the Equalize LPE\$ hypothesis may have resulted because differences in costs were not taken into account. Equalization of net LPE\$, not maintenance of relative gross LPE\$, may be the underlying explanation. The next chapter examines the assumptions of the Equalize LPE\$ hypothesis in more detail.

Chapter 3: Evaluation of Assumptions

Introduction

This chapter examines the effects of the assumptions of the Equalize LPE\$ hypothesis (Ch. 2 ;p. 22-23) on the conclusions of chapter 2. The examinations for each assumption vary from detailed analyses to discussion depending on available data.

Assumptions 1, 3 and 4 apply to both the Equalize LPE\$ and Maintain Relative LPE\$ hypotheses. Thus, investigations of assumptions 1, 3 and 4 consider primarily whether violations may have resulted in the false rejection of the Equalize LPE\$ hypothesis and secondarily whether violations may have given false support to the Maintain Relative LPE\$ hypothesis. Assumption 2 is relaxed in the Maintain Relative LPE\$ hypothesis; thus violations of assumption 2 are considered primarily as possible causes of false rejection of the Equalize LPE\$ hypothesis.

Section one applies a technique called effort standardization to data from the trawl fleet in order to remove possible violations of the assumption that all boats are equal. Section two considers violations of the assumption of equal costs and desirabilities for all areas. Unfortunately, detailed data on area specific costs were unavailable, so section 2 first considers what evidence have been presented thus far that either supports or cast doubt on the assumption that areas are equally desirable. Next, section 2 presents some estimates of differences in costs between vessel size classes and their implications for the assumption of equal area specific costs.

Section 3 uses estimates of steaming times between areas as indices of movement costs to investigate possible violations of the assumption that movement costs are negligible.

Section 4 examines the quality of information and the likely extent of information exchange for four sources of information available to the trawl fleet. A literature review of information exchange in other fisheries is used to draw analogies with and predict the likely amount of information flow in the trawl fleet.

All Boats are Equal

My examination of LPE\$ and effort correlations in chapter 2 were subdivided by horsepower class to eliminate possible confounding effects of vessel size. Vessel horsepower differences between areas may have caused some of the LPE\$ differences shown in chapter 2.

I used a method known as effort standardization to examine the effects of relaxing the all boats are equal assumption on tests of the Equalize LPE\$ and Maintain Relative hypotheses. More specifically, I consider whether differences in catching power among vessels fishing in different areas may have caused the LPE\$ differences that resulted in the rejection of the Equalize LPE\$ hypothesis on the interannual time scale and/or the concordance in the rank of annual RPA's that was consistent with the Maintain Relative LPE\$ hypothesis.

Effort was standardized using vessel horsepower because horsepower has been indentified as a major determinant of fishing power in trawlers by Gulland

(1956a), Beverton & Holt (1957), Houghton (1977) and in British Columbia trawlers by Ketchen & Thomson (1958), Ketchen & Forrester (1966), Kimura (1981), Stocker & Fournier (1984), and Westrheim & Foucher (1985a). This technique has been widely applied to trawl fisheries (see Westrheim & Foucher 1985a for a review). The above studies standardized effort to account for differences in landed weighted per unit effort among different sized vessels. Landed values were first used in fishing power studies by Carlson (1975). Standardization of effort using landed values may yield different results from standardization using landed weight, if for example, smaller vessels landed smaller weights of higher valued species. However, the Equalize and Maintain Relative LPE\$ hypotheses compare LPE\$ among areas and years, not landed weight per effort. Therefore, I standardized effort to account for differences in LPE\$ among vessels. Before proceeding with the process of trying to correct for differences in vessel horsepower among areas, I review evidence concerning the magnitude of differences among areas.

Vessel horsepower has increased in each of the areas over the years 1967-80, and vessel horsepower varies between the seven areas (Fig. 3.1). Table 3.1 presents the results of a Kruskal-Wallis nonparametric ANOVA that indicates that the horsepower differences between areas shown in Figure 3.1 are statistically significant. Similar differences can be shown in other attributes such as length and gross or net tonnage because all are highly correlated with horsepower (Table 3.2).

Data and Methods

DFO saleslip and license data described in chapter 2 were used for the analysis. The main data requirements for the method described below were

Table 3.1. Kruskal-Wallis nonparametric ANOVA comparing vessel horsepower in the seven aggregate areas. Observations are included for each trip made by a vessel to an area. All years (1967-80) have been pooled. H_0 : Areas have the same vessel horsepower.

Area	n	avg.rank
1	3270	9607
2	789	9935
3	6786	5700
4	1456	11946
5	1129	14001
6	4531	11780
7	651	13362
Total n	18612	

Kruskal-Wallis H Statistic = 5622.26, $P < 0.0001$

Table 3.2. Product-moment correlation matrix for four vessel attributes. Observations are included for each vessel that fished during the time period 1967-80. $r = 0.05$ is the value of the correlation coefficient necessary for significance at $P = 0.05$.

Attribute	r value			
Length	1.0			
Netton ¹	0.86	1.0		
Groston ¹	0.86	0.97	1.0	
Hrspwr ²	0.81	0.89	0.90	1.0
	Length	Netton	Groston	Hrspwr

$n = 1326$, $df = 1324$, $r = 0.05 = 0.054$

1 Netton = Net tonnage, Groston = Gross tonnage; both are volume measures. 1 ton = 100 ft³.

2 Hrspwr = Horsepower of the motor

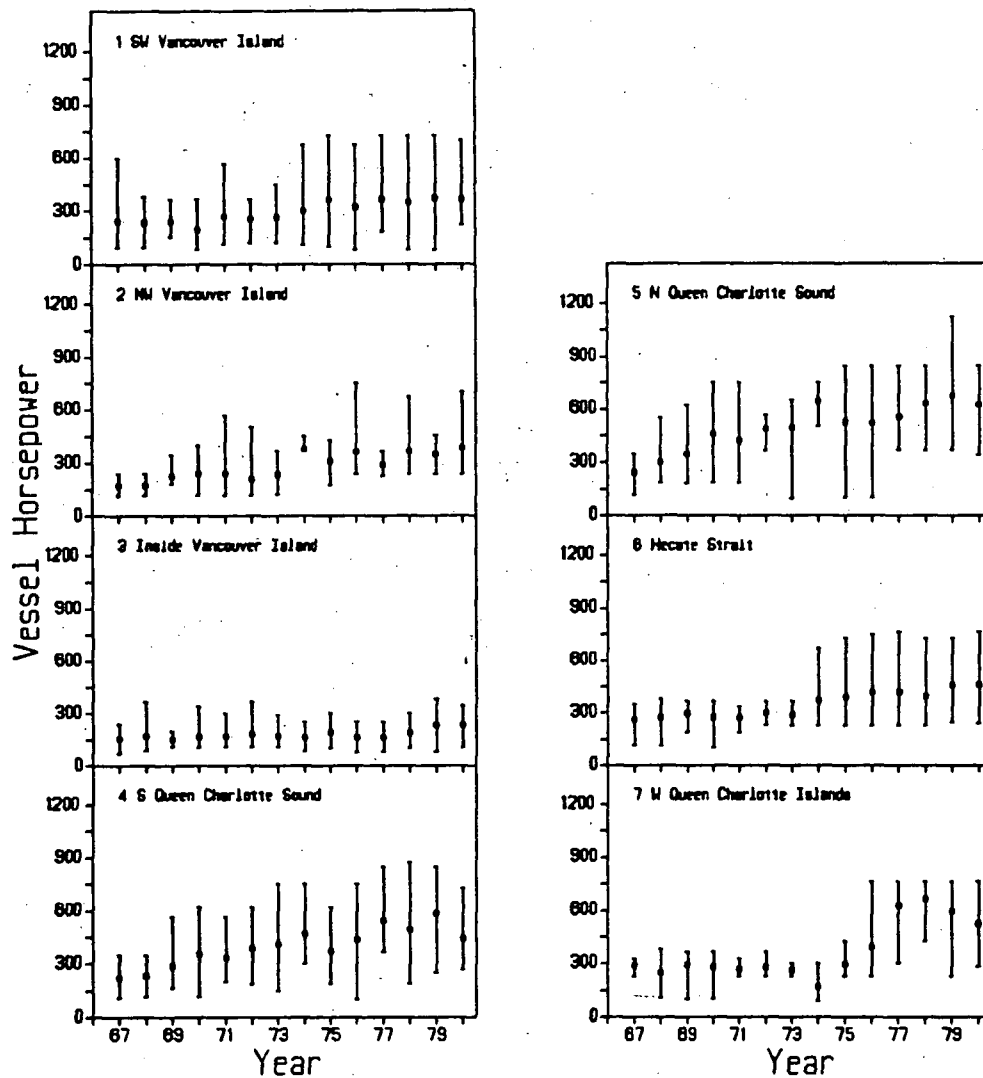


Figure 3.1. Vessel horsepower vs. year for the years 1967-80 in each area. Squares represent means and error bars the interdecile range.

horsepower, landed value of the catch, and effort by vessel and area.

Westrheim and Foucher (1985a) standardized effort for major statistical areas exploited by the British Columbia trawl fleet. My analysis follows their approach with two exceptions: (1) I standardized effort based on landed value

without qualification level rather than landed weight with an 80% qualification level (i.e. Westrheim and Foucher (1985a) included only those trips in which the target species or group constituted 80% or more of the total landed weight), and (2) My space-time stratification is defined by the seven areas and years respectively (see Westrheim and Foucher 1985a, p.1620 for their area-time strata).

Westrheim & Foucher (1985a) used the model of Gulland (1956, p. 5) for deriving estimates of relative fishing power:

$$Y_{ij} = P_i \times t_{ij} \times D_{ij} \times a_j \times \epsilon_{ij} \quad (3.1)$$

where Y =catch of the vessel, P =vessel's absolute fishing power, t = time spent fishing, D =density of fish, a =vulnerability of the fish, ϵ =a random error term, and the subscripts i and j refer to the vessel and area/time period respectively. Landed weight per effort, ($LPUE = Y_{sj} / t_{sj}$), of a "standard" vessel is substituted for $a_j \times D_j$ when these two factors are unknown.

Relative fishing power (RFP) is then calculated as:

$$RFP_i = \frac{LPUE_{ij}}{LPUE_{sj}} \quad (3.2)$$

Although Westrheim & Foucher (1985a) used the same underlying model as Gulland, their application methods differed. Gulland used a log-transformed version of equation 3.1 and applied it to individual vessels in restricted area-time cells. Westrheim and Foucher (1985a) calculate the RFP of vessel horsepower classes for selected species groups and broad area-time cells. My analysis involves

large aggregate areas and years, so I chose to follow Westrheim and Foucher's (1985a) method.

Substituting LPE\$ for LPUE, and landed value for landings, the method has four steps (see Westrheim & Foucher 1985a, p.1623):

1. Compile landed values, nominal effort and LPE\$ by horsepower class, area, and year.
2. For each area select a standard horsepower class based on the number of years it fished, cumulative value of landings, cumulative days fished, and cumulative number of trips made.
3. Calculate mean RFP for each horsepower class as:

$$\overline{\text{RFP}}_i = \frac{1}{n_i} \sum_j \frac{\text{LPE\$}_{ij}}{\text{LPE\$}_{sj}} \quad (3.3)$$

where $\overline{\text{RFP}}$ = the mean relative fishing power, n = the number of years of records, LPE\$ = the landed value per days fished, and i and j are the horsepower class and year, respectively.

4. Regress $\overline{\text{RFP}}$ on horsepower class to correct for horsepower classes with small values of n_i and recalibrate to the standard horsepower class:

$$\text{RFPu}_i = a + b \text{ (horsepower class } i) \quad (3.4a)$$

$$\text{RFPc}_i = \frac{\text{RFPu}_i}{\text{RFPu}_s} \quad (3.4b)$$

where RFPu = uncalibrated estimate of relative fishing power, RFPc = calibrated estimate of relative fishing power, a and b are regression parameters and i and s denote horsepower class and standard respectively.

Westrheim and Foucher (1985a) arbitrarily excluded from the regression any horsepower classes that fished only a few years. I performed weighted regression using all the data, where the regression weights were the number of years that each horsepower class fished. Horsepower classes that fished only a few years were included, but were given less weight in the regression in favor of horsepower classes that fished during more of the time series.

Using the predicted RFPs from the regressions, the standardized effort is determined for each horsepower class, area, and year as:

$$SE_{ikj} = NE_{ikj} \times RFP_{ik} \quad (3.5)$$

where SE=standardized effort, NE=nominal effort, and i, k , and j denote the horsepower class, area, and year, respectively.

The standardized effort for each area and year is:

$$SE_{kj} = \sum_i SE_{ikj} \quad (3.6),$$

where all symbols are as above. Note from equation 3.5 that horsepower classes greater than the standard had RFP's greater than 1.0 and greater standardized effort than nominal effort, while for horsepower classes less than the standard, RFP's were less than 1.0, and the converse was true. Thus areas with larger vessels had lower standardized LPE\$ than nominal LPE\$ and vice versa for areas with smaller vessels (see below).

Results

Figure 3.2 shows the regressions of step 4 for each of the seven areas. Horsepower class accounted for 30-90% of the within area variation in \overline{RFP} . The poor fits in Areas 2 and 7 are probably due to the low effort exerted annually in these areas that results in greater variability in the LPUE values for different horsepower classes.

The effect of using standardized rather than nominal effort on the LPE\$ values for each area is shown in Figure 3.3. Area 5 showed the greatest difference between nominal and standardized LPE\$. As expected, the standardized LPE\$ is less than the nominal LPE\$ in most areas, except notably area 3 where standardized LPE\$ is greater because most of the effort in area 3 is exerted by small horsepower classes with relative fishing power less than 1.0.

I also re-examined the annual numerical responses of Figure 2.10 using the standardized effort and LPE\$ values. Only the regression for area 7 retained its significance ($r^2=0.44$, $P<0.01$). However, as before, the relationship is confounded by time trends in the standardized variates and the slope of the regression of the time trend residuals was not significant ($r^2=0.18$, $P<0.16$).

How does effort standardization affect how well the data agree with the two LPE\$ hypotheses? The concordance measure for the standardized LPE\$'s shown in Figure 3.3 is only slightly less than the concordance for nominal LPE\$ (0.61 versus 0.67; cf. Fig. 2.12). Thus it is unlikely that vessel catching power differences resulted in the false rejection of the Equalize LPE\$ hypothesis in Chapter 2. The standardized RPA's are shown in Figure 3.4. Effort standardization reduces the between-area differences in RPA, but again the

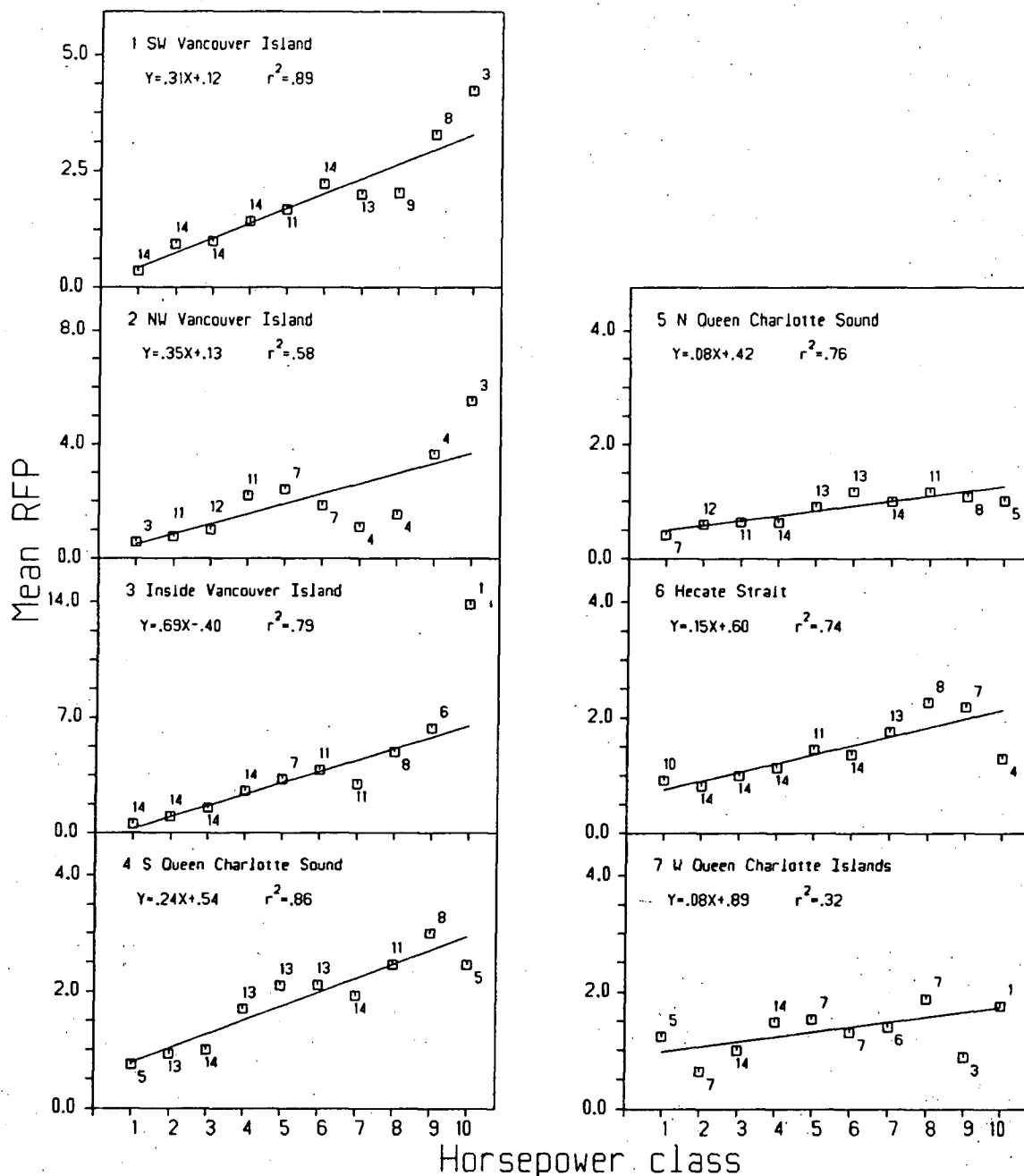


Figure 3.2. Mean relative fishing power vs. horsepower class for each of the seven areas. Regression lines, their equations and their r^2 values are shown for each area. Numbers beside squares are the number of years that each horsepower class fished in the respective areas.

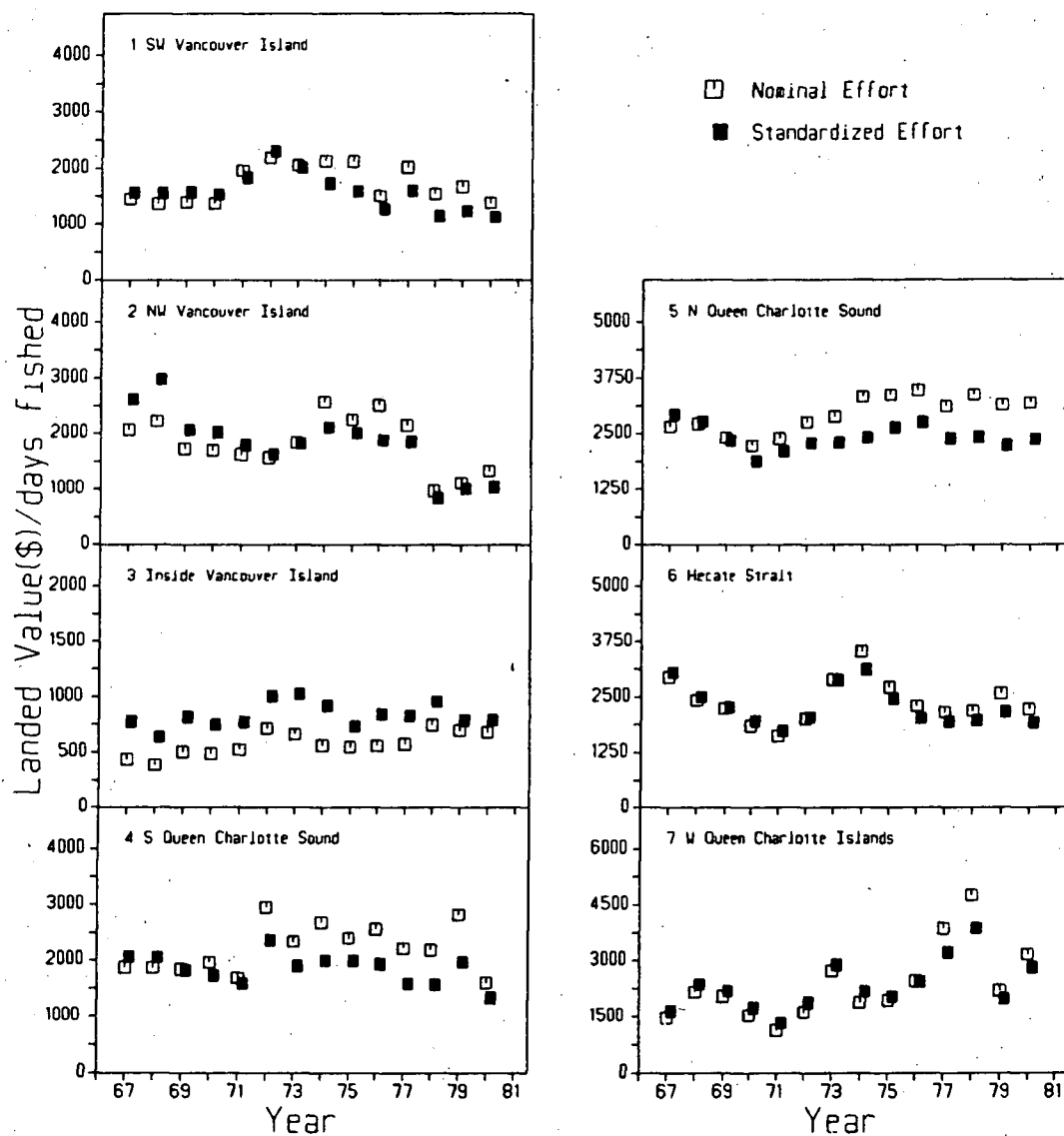


Figure 3.3. Nominal and standardized landed values(\$)/(days fished) vs. year for the years 1967-80 in each area.

concordance in rank was only affected slightly, changing from 0.67 to 0.61. While fishing power differences exist between vessels fishing in different areas, taking account of them has only slightly reduced the differences in LPE\$ between areas and has not changed the qualitative results. However, the standardization of effort is directed at removing vessel size effects on indices of gross LPE\$,

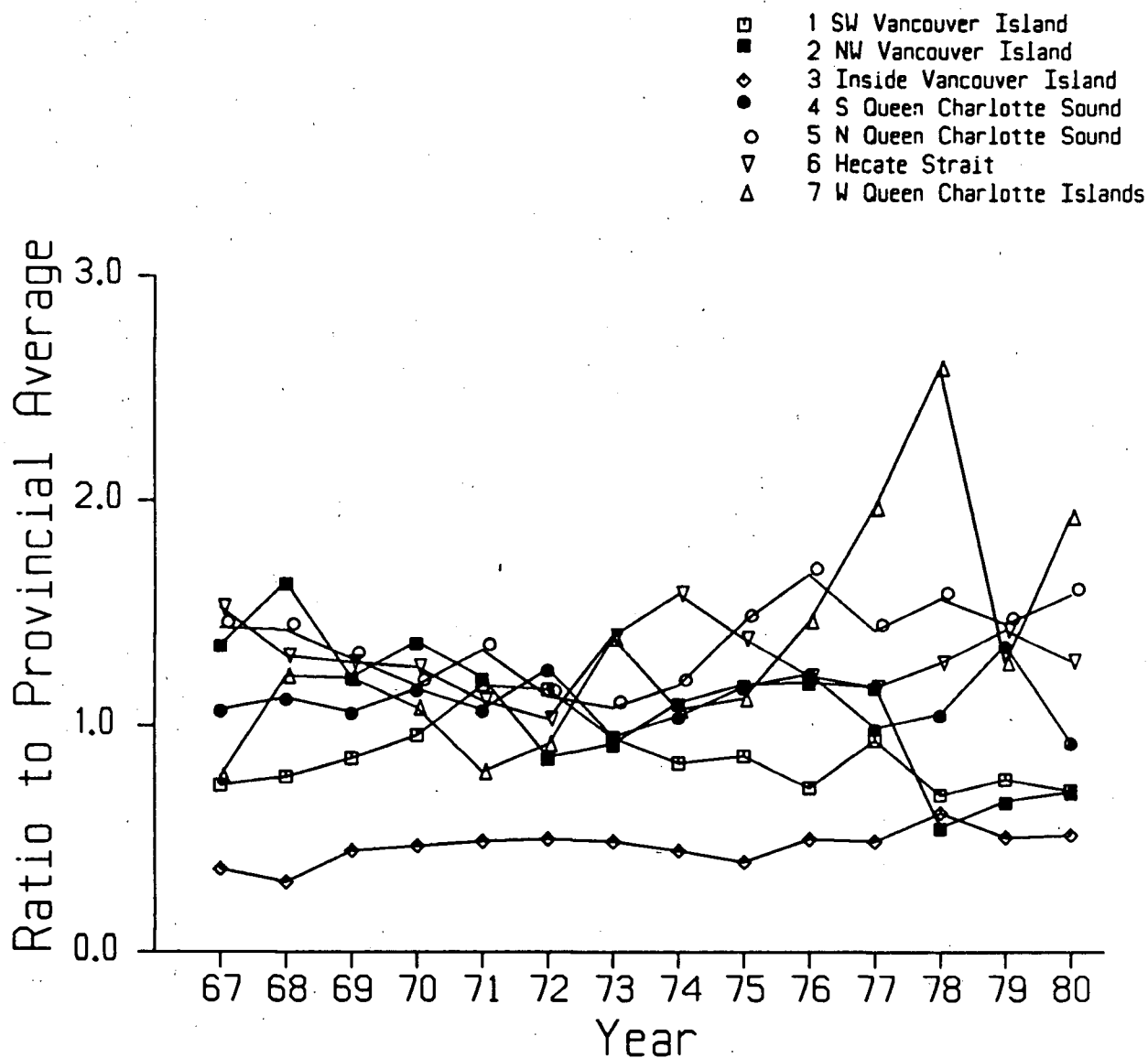


Figure 3.4. Ratio to provincial average calculated using standardized landed values(\$)/(days fished) vs. year for the years 1967-80 in each area.

and does not account for effects of vessel size on other factors such as fishing costs or overall mobility. The possible effects of fishing costs will be considered in the next section.

Equal Costs and Desirabilities of Areas

The assumption of equal costs and desirabilities is relaxed in the Maintain relative LPE\$ hypothesis, but the assumption is essential to the Equalize LPE\$ hypothesis to account for costs and *noneconomic* factors that may affect a skipper's choice of one area over another. This section first considers whether results presented thus far suggest that areas have equal desirabilities. Next, it presents some estimates of differences in costs between vessel size classes and their implications for the equal cost assumption.

Desirability is an ambiguous term, but in the fisheries context, factors that affect the desirability of areas include (1) protection from or exposure to weather, (2) distance to home port, (3) personal preference based on past experience, (4) risk of gear damage, (5) available species and markets (6) depth distribution of available species and other intangibles that are not accounted for by the LPE\$ benefit measure. I have presented some evidence that suggests areas differ in their desirabilities. One example is the high concordance in rank of the proportion of effort allotted to each area annually. The concordance for effort is higher than for RPA, which coupled with the weak annual numerical responses (Fig. 2.10) suggests that the fleet is not simply allotting their effort strictly in response to some constant relative benefit. Other factors not included in the benefit measure may be important (i.e. desirabilities and costs).

In addition, a large proportion of total coastwide effort is consistently exerted in area 3 (Fig. 2.2), despite an unpredictable LPE\$ pattern, and higher

and more predictable LPE\$s in adjacent areas (Fig. 2.8). Area 3 does have attractions: it is close to Vancouver, its waters are sheltered from major storms by Vancouver island, and its proximity to markets lets fishermen have a more regular work schedule. This latter quality is apparent in the the very consistent intra-annual pattern of effort in area 3 (Fig. 2.8). However, the apparent desirability of area 3 to smaller vessels may be dictated by undesirable qualities or the operational dangers of the other areas. Small vessels are limited to periods of relatively calm weather on the adjacent offshore areas (i.e. areas 1,5) and large steaming distances preclude trips to the other areas (e.g. areas 4-7). The revenue from a filled hold on a small vessel might not offset the fuel costs for travelling such distances.

The second part of the assumption is equal fishing costs of the areas. The most significant and consistent fishing cost (excluding movement costs and unpredictable costs due to gear damage or equipment breakdown) is the cost of fuel for trawling and movement within areas. If the number of hours trawled is proportional to the number of days fished, my gross LPE\$ values for each area should be roughly proportional to the Net LPE\$. However, equalizing gross LPE\$ is only equivalent to equalizing net LPE\$ under the assumption of equal fishing costs in the areas. Therefore, if my rejection of the Equalize LPE\$ hypothesis was due to violations of the equal area specific cost assumption, I must show differences in the area specific costs that are proportional to gross LPE\$. One factor that could result in costs that are proportional to gross LPE\$ is the difference in vessel horsepower among areas shown in the previous section.

Padilla (1986) presented a table of costs per vessels-ton-day for three length categories derived from a sample of 59 B.C. trawlers taken in 1982. His figures are hard to interpret however, because length and tonnage are highly

Table 3.3. Estimated variable and total costs per days fished for three vessel length categories in 1982.*

Length(ft)	Variable ¹ cost(\$)/day	Total cost(\$)/day
<64	1067	1447
65-84	2336	3244
>85	5129	6311

* Modified from Padilla (1986).

1 Includes crew share, provisions, fuel, oil, and grease.

correlated (Table 3.2), and he did not present the raw data. In an effort to reinterpret his data, I used the 1980 attribute data to calculate the mean gross tonnage for each of his vessel length categories and multiplied these values by his cost figures to obtain costs per day fished for each length category (Table 3.3).

Although these figures are approximations, they clearly show both total and variable costs increase with vessel size. Thus, it is likely that including vessels' fishing costs would reduce differences in net landed value per day fishing between areas, because of vessel size differences between areas. In the case of effort standardization this reduction in LPE\$ differences between areas was slight. Therefore, it is unlikely that accounting for costs due to vessel size differences would result in a failure to reject the Equalize LPE\$ hypothesis.

Other differences between areas such as trawling depth, local currents and type of bottom could affect the relative costs of trawling per hour. There are insufficient data to predict what effect these factors have on the relative magnitude of area specific costs.

Movement costs within areas and costs of searching are probably related to the size of the areas and the proportions of bottom that are trawlable. The costs of movement within areas are probably small relative to the cost of trawling, because: (1) most trawling grounds are well known to most trawlers, (2) navigational aids such as Loran provide accurate and repeatable location information and (3) searching is often combined with trawling to offset costs. However, the ratio of trawling cost and searching cost undoubtedly varies considerably with conditions such as abundance and availability of fish, target species, bottom type, and experience of the skipper.

In conclusion, areas probably differ in fishing costs, because of differences in many of the above factors. The equalize LPE\$ hypothesis is most sensitive to violations of the assumption of equal desirabilities and costs but violations should not effect the Maintain Relative LPE\$ hypothesis unless the relative area-specific costs and desirabilities vary over time. However, the evidence presented is insufficient to predict the quantitative effects of accounting for fishing costs in each area. Qualitatively, accounting for differences in costs due to vessel size differences among areas, would reduce differences in net landed value per day fishing between areas which would be consistent with an Equalize Net LPE\$ hypothesis.

Negligible movement costs

Given the large aggregate areas and the existence of only two major landing ports at opposite ends of the province, movement costs are substantial, not negligible. Furthermore, costs of movement within the areas are probably small in comparison to the costs of steaming to and from port. This section first considers the impact of movement costs on movement patterns. The second part presents estimates of steaming times (a gross measure of movement costs) and their implications. I was unable to include a detailed analysis of the effects of movement costs for lack of data.

For Vancouver based vessels, the cost of steaming to the northern areas is much greater, so the major decision is whether to fish the Areas 1 or 2 on the west coast of Vancouver Island or the northern areas (4-7). Given that most of the fleet fishes out of Vancouver, I expect movement costs to force vessels to be more selective in their choice of when to fish the northern areas as compared to the southern areas. The pattern found in the consistency of numerical responses supports this assertion.

Two areas in Queen Charlotte Sound had the most consistent numerical responses, while area 3 had the least consistent numerical response and areas 1,2 and 6 were intermediate (Fig. 2.9). The less consistent numerical response in area 6 compared to areas 4 and 5 may result from the greater number of stationary vessels based in Prince Rupert that fish in area 6 (Table 2.2). The low consistency of area 7, is probably due to the low amount effort exerted in

this area (Fig. 2.2), and the areas exposure to greater extremes of weather. It is apparent that movement costs are different between areas and that these differences have had some effect on the observed vessel movement patterns.

To examine the effects of movement costs, I estimated the total steaming times from home port to each area (and back) for all vessels each year. The steaming times are based on the distances from each port to each of the areas assuming a steaming speed of 10 knots (D. March, B.C. Trawlers' Association, pers. comm.). I then divided these total times by the number of days fished in each area. If movement costs are responsible for the rejection of the Equalize LPE\$ hypothesis, then steaming times/(days fished) (STPE) should be proportional to the LPE\$ in each area.

On the average, areas with higher gross LPE\$ also have greater STPE and higher proportions of larger vessels (Table 3.4). While there are exceptions (e.g. areas 2 and 6 have relatively higher and lower steaming times for their LPE\$, respectively) to this general trend, Table 3.4 suggests that the inclusion of movement costs would tend to reduce differences in net economic attractiveness among areas. Similarly, on an annual basis, LPE\$'s are positively correlated with STPE's in 6 of the 7 areas (Fig. 3.5). If movement costs were included annual differences in LPE\$ between years in each area would also be reduced.

The correlations between LPE\$ and STPE in Figure 3 are not perfect (i.e. only 4 of the positive correlations are significant ($P < 0.1$)), but STPE is only a crude measure of movement costs. I have estimated steaming times to the major ground in each area, or to the center of areas with several grounds (e.g. Area 6, Hecate Strait), but the areas are quite large so actual steaming times might vary around these "average" estimates. Also, cost of steaming varies with vessel

Table 3.4. Average standardized LPE\$'s, steaming times/(days fished) (STPE), and vessel horsepower for each area and the years 1967-80.

Area	LPE\$	STPE (hrs)	Horsepower
1	1427	5.8	309
2	1685	14.8	312
3	756	4.2	194
4	1699	11.6	402
5	2225	13.2	503
6	2091	11.5	367
7	2098	17.1	482

size, the amount of fish aboard, and may have even varied with vessel size over the years as newer, more fuel efficient vessels entered the fishery. Despite these factors, the qualitative effect of including movement costs is to reduce differences in LPE\$ between areas, and reduce differences in LPE\$ between years within areas. The evaluation of movement costs does not support either LPE\$ hypothesis over the other. Nevertheless, Table 3.4 and Figure 3.5 suggest that movement costs are an important consideration in the trawl fleet, and that equalization or maintenance of relative Net LPE\$ may be the net result of movement patterns.

Perfect Information

Both the LPE\$ hypotheses rely on vessel movements in response to perceived benefits to either equalize or maintain relative LPE\$. The amount and

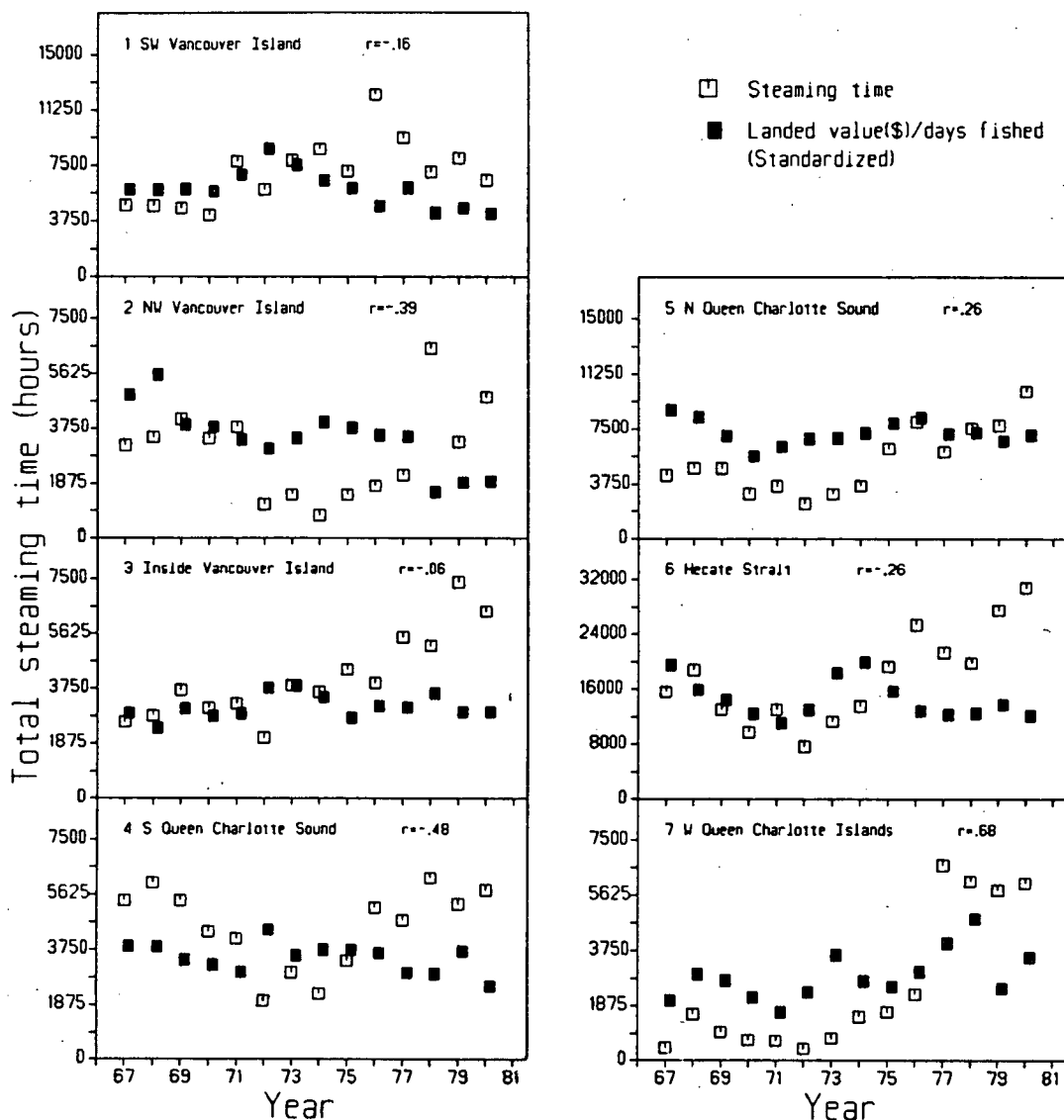


Figure 3.5. Steaming times/(days fished) and standardized landed values(\$)/(days fished) vs. year for each area. Product moment correlation coefficients (r values) are shown for each area. Two stars (**), one star (*), or NS indicate significance at $P < .05$, $P < 0.1$, or not significant respectively. Note: Scale for landed value(\$)/(days fished) is the same as Figure 3.3.

quality of information affects fishermen's perceptions and presumably influences their choice of fishing location. There are several sources for such information and I will briefly discuss four of these below.

1. Historical data
2. Personal experience of the skipper or crew
3. Processing plants
4. Other fishermen

Historical data

Some of the trawling grounds off British Columbia have been exploited since 1912, and the Fisheries Research Board of Canada has kept records of trawlers since 1944 (Lippa 1967). Reports of monthly landing by species and statistical area are available from university libraries. The locations of many of the traditional fishing grounds are clearly marked on most nautical charts. Reports of exploratory trawl surveys conducted by the Department of Fisheries and Oceans are commonly sent to participating and/or interested fishermen. I am not certain of the extent to which fishermen use historical data, but it is likely that from a combination of the historical sources and conversations with willing oldtimers, an inexperienced trawler could gain general knowledge on seasonal distributions of species in each of the areas. However, these sources do not provide the timely information concerning catch rates in specific areas needed to respond to within and between trip changes in abundance.

Personal Experience

Personal experience is perhaps the most trusted source of information because it does not depend on the opinions of others. Personal experience may

be a particularly valuable source of information on general seasonal patterns of availability in particular areas, but it is limited to the experience of the skipper and possibly crew members if they have worked previously on other vessels. Personal experience cannot provide within-year information of catch rates in areas other than those fished by the given skipper, and therefore as a sole source of information it would likely result in quite restricted movement patterns for most vessels.

Plants and Other Fishermen

Of the four information sources, plants and other fishermen have the greatest potential to provide the timely information on catch rates needed to choose the "best" fishing location.

Before discussing these information sources, it is relevant to consider: What is perfect information from the individual vessel perspective? Figures 3.6 (cf. Fig. 2.8), 3.7 (cf. Fig 3.4 open squares), and 3.8 attempt to quantify the information that would be available in a scenario where each vessel knew the LPE\$ obtained and area fished by every other vessel. On both the among season (Fig. 3.6), and within season (Fig. 3.7) time scale, this complete information sharing scenario provides some clues about which areas are on average better than others and the relative predictability of seasonal LPE\$'s in each area. The value of the perfect state depends on the ability of the skipper to discern these patterns from the rather variable individual observations (Figs. 3.6, 3.8). The spatial areas chosen by skippers (ie. fishing grounds) are smaller than these larger aggregate areas, but these figures at least present a rough idea of the level of information available on the spatial and temporal scales over

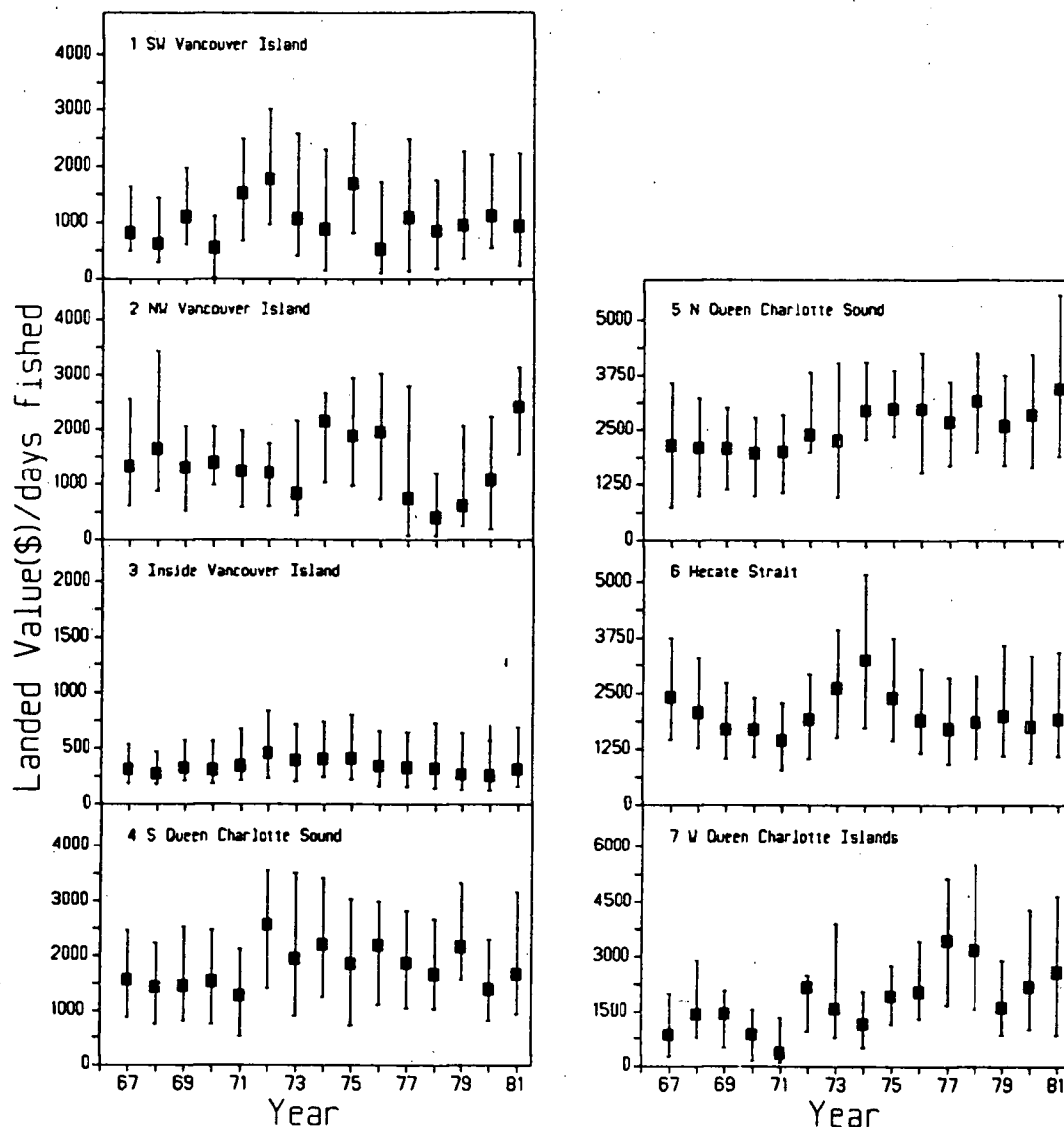


Figure 3.6. Landed value(\$)/(days fished) vs. year for each area. Squares are medians over vessels and error bars the quartiles for the years 1967-81.

which fishermen make major decisions. Deviations from the perfect information state depend on the amount and quality of information exchanged either between processors and fishermen, or among fishermen. Some indication of the amount and quality of information exchanged comes from anthropological studies.

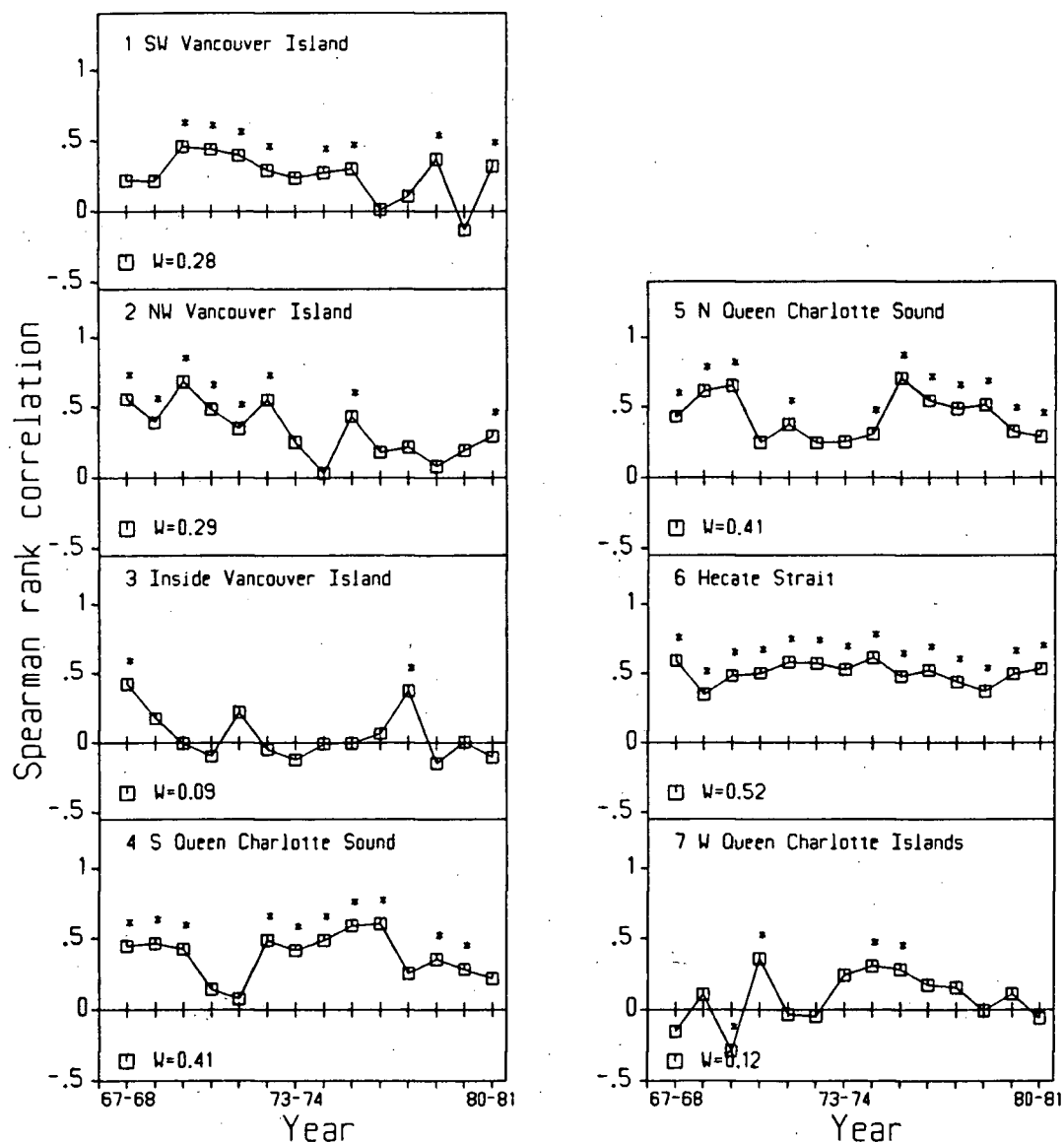


Figure 3.7. Spearman rank correlations (r_s) for weekly landed value(\$)/(days fished) (medians over vessels) in consecutive pairs of years 1967/68 - 80/81 in each area. Stars (*) indicate significance at $P < .05$. Kendall's Concordance(W) values are recorded on each plot. Concordances are significant at $P < .01$.

Fishing operations are often vertically integrated with company owned boats directed to some extent by plant managers (e.g. Andersen 1972, 1973). In

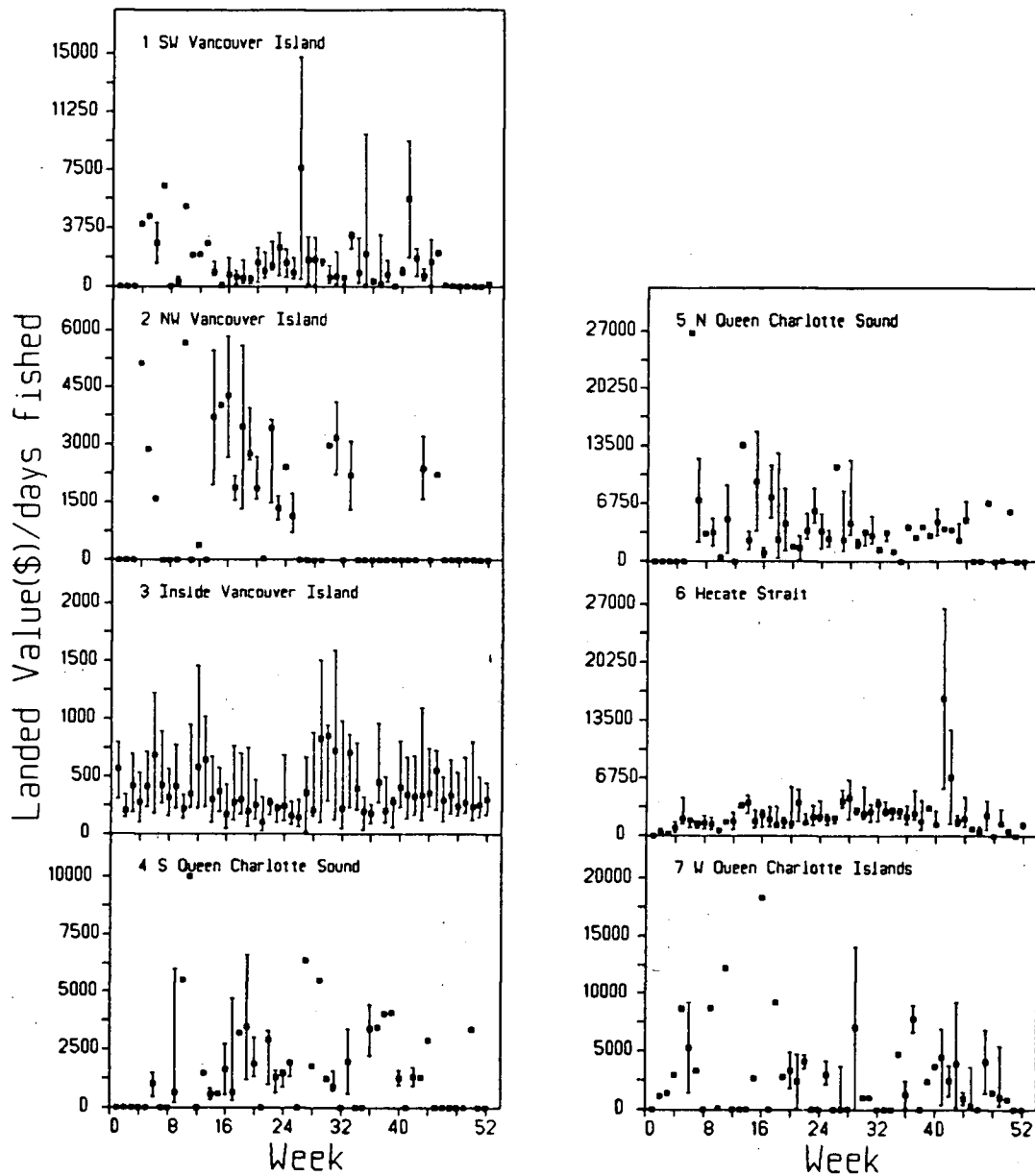


Figure 3.8. Landed value(\$)/(days fished) vs. week for each area. Squares are medians over individual vessels and error bars the quartiles for the years 1967-81.

such cases, there is cooperation between the fleet and plant managers. Plants provide advice about species and areas in exchange for catch estimates (called

hails) from skippers. Some plants may monitor catch hails and plot the information on charts available to all skippers who fish for the plant (Andersen 1972). The utility of catch hails and locations depends on the accuracy of the catch hails. Andersen (1972) found the accuracy of catch hails for Newfoundland trawlers was inversely related to the number of days left in the trip because skippers were reluctant to give away any information that might jeopardize their current trip.

The British Columbia trawl fishery has some vertically integrated plant/vessel operations. There are also fishermen cooperatives where vessels are often operator owned. In these cases, fishermen have more freedom, but there may be less information sharing with plants. I expect that the amount of information exchange between plants and fisherman in terms of location and species would be greater in vertically integrated operations. In any case, plant-vessel information is limited to vessels with the same plant and therefore still only represents a subset of the available information.

Information sharing among fishermen has been the subject of much anthropological study. Orbach (1977) found most tuna seiners were involved in some communication system. Seiners formed "code groups" that shared information concerning the location of tuna schools using elaborate codes to prevent non-group members from stealing information. Information groups were formed for a combination of economic, social, and status purposes, but the main reason was probably economic because the tuna range over 5,000,000 square miles and information sharing considerably reduces searching costs. Similarly, Gatewood (1984) found Alaskan salmon seinermen formed small groups that shared information as they searched for salmon just in advance of fishery openings.

Stuster (1978) suggested differences in information sharing varied with the type of fishing strategy. He thought "trapper fishermen" (e.g. lobster, crab trappers, and set line fishermen) were the least likely to share information, while "hunter" fishermen (eg. trollers, harpooners, seiners) that actively pursue migratory species were most likely to share information. He found trollers for albacore were in the hunter category and they formed code groups. Stuster placed California trawlers in the trapper category and gave anecdotal accounts of how they practice deception, and work alone to protect the location of "hot" spots. Stiles (1972) found Newfoundland longliners practiced "radio camouflage" by avoiding specific statements of results or intentions.

Based on observations of Newfoundland deep sea trawlers, Andersen (1972) concluded that much of the information exchanged between skippers was purposely distorted and deceptive. Distortions included underestimation of catch by as much as 50% when fishing was good, and overstatement of the catch when fishing was poor to trick competing skippers into steaming to a new position in the expectation of better fishing. Deceptions included misinformation concerning bottom snags, fishing depth and location, and radio silence to preserve exclusive rights to a particularly good location. Andersen (1972) also identified certain non-deceptive transactions including discussions of trawling strategy among 2-3 trawlers from the same plant when they were fishing in the same area but at some distance from other vessels, and "donations" by successful skippers of good fishing locations after another skipper had a run of bad luck.

Andersen (1972) identified four key factors that were responsible for the deceptive patterns of information exchange among Newfoundland trawl skippers. The first was the unequal distribution of catch values between skippers both within and between plants. Each plant had poor fishermen and top fishermen or

"highliners", and the highliners always received the best boats and crew from the plant. The second factor, was the occurrence of bad breaks (e.g. equipment breakdown, accidents) that were more frequent on the older vessels and that made older vessels less desirable to skippers and crew. The third factor was uncertainty in hunting a common property resource. Although skippers can at times detect their prey with electronic devices such as echo sounders, results of efforts are never certain until the trawl is retrieved. The uncertainty was compounded by competition from other domestic trawlers and foreign fleets and it accentuated the importance of local knowledge. Andersen argued these three factors alone did not lead to the misinformation he observed.

The most important factor contributing to the deception was the co-adventure nature and vertical integration of the fishing operations. The co-adventureship occurred on two levels; between plants and skippers and between skipper and crew. At the first level there were formal and informal contracts that stated that the plant provided gear, crew and determined skippers on their vessels. This resulted in rewards of better vessels and crew for successful skippers. Skippers were responsible for the crew, choice of fishing area, and within trip storage of fish. Crew were paid on a share system based on a proportion of the revenue from each trip's catch. It was the system of co-adventureship that acted in combination with the other three factors to make it in each skipper's economic interest not to exchange any information that might jeopardize his catch relative to others.

The British Columbia trawl fishery has a similar organization to the Newfoundland trawl fishery, and while the plants and vessels may not be vertically integrated to the extent mentioned above (e.g. especially the fishermen's cooperatives), the pattern of rewards to successful skippers can occur from both

free movement of crew between vessels, and from highliners' greater abilities to purchase new vessels or upgrade equipment on existing ones. Thus, incentives for disinformation rather than information sharing exist, and my personal experience with British Columbia trawl skippers indicates that radio silence and catch underestimation are not unique to Newfoundland trawlers.

I have presented anecdotal evidence supporting violation of the perfect information hypothesis, but I cannot quantify the affect of violations on the LPE\$ hypotheses. One recent study, that modeled information exchange in a fishing system, may shed some light on the expected effects of disinformation on movement patterns.

Allen and McGlade (1986) considered movement and information exchange in a model that they applied to Nova Scotian trawl fisheries. The model considered two groups of fishermen: *stochasts* and *cartesians*. Stochasts were characterized as high risk takers who fished according to some personal or random scheme and who were only weakly influenced by information from others. Cartesians were unwilling to take risks, and fished only in areas promising the best *known* returns. One scenario compared the two groups under conditions of no information sharing between groups. When cartesians withheld information from stochasts, there was little effect on the movement patterns or general success of each group, but if the situation was reversed, the cartesians perished. In another scenario, weak mutual exchange of information was found to be beneficial to the fleet as a whole. While in reality there is undoubtedly a continuum of strategies between the two extremes, the study suggests that a poor information state favors vessels with greater movement, and as long as there is some weak level of information exchange, vessels will discover and move to areas of high catch rates.

Summary of Evaluation of Assumptions

The major results of the evaluation of assumptions are:

1. Accounting for vessel size differences slightly reduces differences in area LPE\$'s.
2. Inclusion of area specific costs would reduce differences among area LPE\$'s because of difference in vessels size between areas and in costs between vessel sizes.
3. Accounting for movement costs would reduce average differences in LPE\$ between areas, and differences in LPE\$ between years within each area.
4. Disinformation is probably common in the trawl fishery, but fleet responses to catch rates may depend only on a few highly mobile vessels and weak information exchange.

The results indicate that assumptions 1-3 of the Equalize LPE\$ hypothesis have been violated and that accounting for violations (especially differences in costs) would result in smaller differences in LPE\$ between areas and between years within areas. The evaluation of assumptions does not provide unequivocal support for either LPE\$ hypothesis, but instead points to the importance of including costs in movement studies. The evaluation also suggests that equalization or maintenance of relative net LPE\$ may be the underlying result of and impetus for movement patterns. However, a more detailed accounting of costs is required to distinguish between these two alternatives.

Chapter 4: Discussion of Effort Distribution Analyses

Introduction

Section one of this discussion compares my findings with Hilborn and Ledbetter (1979) and Millington (1984), and attempts to draw some generalizations from these three movement studies. Section two discusses some data and statistical problems common to the three studies and to fisheries data sets in general. Section three considers some general implications of movement pattern studies.

Other Applications of the Hilborn-Ledbetter Hypotheses

My comparison will focus on five aspects of the fleets in an attempt to draw some generalizations between fishery characteristics and movement patterns.

The five factors are:

1. number of vessels
2. availability of information on catch rates and/or abundance to to fishermen
3. ratio of mobile to non-mobile vessels
4. type of management regulations
5. movement hypotheses considered "best"

Hilborn & Ledbetter's (1979) study on the salmon seine fishery included about 500 vessels. Information on abundances is provided to those vessels in the form of preseason forecasts published by the Department of Fisheries & Oceans, and area specific catch rates are available from the large number of vessels fishing each week. The ratio of mobile vessels (defined as vessels fishing more

than one of their eight aggregate areas) to stationary vessels varied between 5:1 in 1973 and 12:1 in 1976. Management regulations consisted of short area/time openings of 2-4 days over a season that lasts from May to November (Hilborn and Ledbetter 1979). Hsu (unpublished data, cited in Hilborn and Ledbetter 1979) suggested that seiners moved in traditional patterns, but Hilborn and Ledbetter did not explicitly test the traditional patterns hypothesis. They dismissed the existence of traditional patterns based on differences in numerical responses between years. However, I found that movement in traditional patterns by trawlers does not necessarily imply similarity in numerical responses between years (e.g. Area 3, Figs. 2.7 & 2.9). Their study clearly rejected the Equalize LPE\$ hypothesis on both a between and within year time scale. They concluded that differences in LPE\$ between areas were due to a combination of economic and relative noneconomic desirability, and boat movement tended to maintain annual ratios of each areas LPE\$ to provincial average LPE\$ (i.e. RPAs, the Maintain Relative LPE\$ hypothesis). They supported their conclusion with an example where salmon enhancement resulted in increased total stock available in one area, and these fish attracted more vessels that maintained the area's relative LPE\$. They did not consider the Maintain Relative LPE\$ hypothesis on a weekly time scale and their study involved four years.

The salmon gillnet fishery examined by Millington (1984) consisted of about 2500 vessels, some of which also participated in the salmon troll fishery. Gillnetters have access to the same preseason forecasts as seiners, and their larger numbers may mean better inseason catch rate information. Most of the stationary boats fished in one area (Area 29, Fraser river; for a map of statistical areas see Millington 1984 p. 23-24), where they were outnumbered by mobile vessels by a 2:1 ratio. In all of Millington's other areas combined, the

mobility ratio averaged about 20:1 over the three years examined. Unfortunately, because Millington considered smaller areas, his ratios are not comparable with those of Hilborn and Ledbetter or my study. Without a re-analysis of Millington's data and ignoring the special case of area 29, I estimate a comparable ratio for aggregate areas would be bounded by the estimates for area 29 and the other areas, and is probably about 4:1. Management regulations in the gillnet fishery are similar to those in the seine fishery, but openings tend to be shorter (1-2 days) because gillnetters fish more in river mouth areas where salmon are more vulnerable.

Millington's (1984) test of the Traditional patterns hypothesis was a comparison of the probabilities of vessels fishing particular area pairs. He concluded that the nearly constant probabilities for adjacent areas were due to geographical proximity and that the interannual differences of probabilities for area pairs that were separated by larger distances were due more to changes in strengths of salmon runs. He did not examine within year effort distributions because he thought his time series was too short, and the reasons (e.g. regulations) for unexpected changes in these effort distributions would have been hard to isolate.

Like Hilborn and Ledbetter (1979), Millington (1984) clearly rejected the Equalize LPE\$ hypothesis. Annual RPAs did not maintain consistent rank between years, but overall ranks appeared to be related to movement costs (i.e. remote areas had the highest RPAs and areas close to major ports had the smallest RPAs consistent with the Maintain Relative LPE\$ hypothesis).

Millington (1984) attempted to forecast weekly boat numbers based on the Equalize LPE\$ and Maintain Relative LPE\$ hypotheses and found neither model

performed much better than the historical mean effort level except in one centrally located area (area 8). He also found the median LPE\$ of the first and last week each boat fished (that he called the starting and stopping LPE\$s) were nearly equal in two of the three years studied and concluded that similar economic criteria were used by the fleet as a whole in determining when to start and stop fishing each season. However, distributions of starting and stopping LPE\$ for individual vessels differed indicating that starting and stopping times were modified by traditional patterns (i.e. some vessels likely started and stopped in the same weeks each year regardless the LPE\$).

Millington's (1984) study essentially found none of the hypotheses explained movement patterns very well, although based on his attempted forecasts, historical patterns were better predictors of within year patterns than methods based on either of the LPE\$ hypotheses. As Millington (1984) acknowledged, his between year comparisons might have been improved if he had been able to include years that covered a full life cycle of salmon abundance (especially for sockeye salmon).

The number of vessels fishing in the trawl fishery averaged about 100 over the study period. The ratio of mobile to nonmobile vessels was 1.3:1, but mobile vessels accounted for most of the landed catch, value and effort expended (Table 2.2). As in Millington's (1984) study, stationary vessels were particularly prevalent in one area (area 3). The lack of preseason forecasts, small vessel numbers and low mobility result in a much poorer information state than in either of the salmon fisheries.

In comparison to the salmon fishery, the trawl fishery was virtually unregulated over the study period, and what regulations were in effect (i.e. catch

quotas) were not strictly enforced (because they were not enforceable within the Fisheries Act at that time). However, there were some isolated seasonal closures to protect spawning aggregations of various species, particularly in areas 1 and 3. Plants have also sporadically imposed miscellaneous regulations, such as trip quotas on certain species or minimum sizes (for economical filleting), but these are largely undocumented and it is difficult to evaluate their impact. The trawl fishery essentially operated year-round in a generally unrestricted regulatory environment.

Unlike the two salmon studies, I failed to reject the traditional patterns hypothesis on the annual time scale, and on the within season time scale for one area (area 3). However, my methods for examining traditional patterns differed from both of the previous studies. Like both salmon studies, I clearly rejected the equalize LPE\$ hypothesis. And finally, like Hilborn and Ledbetter, but unlike Millington, I failed to reject the maintain RPA hypothesis on an annual time scale, but was able to reject it on a weekly time scale.

My study examined evidence for possible violations of the assumptions of the Equalize LPE\$ hypothesis. The examination suggested my rejection of the Equalize LPE\$ hypothesis may have been due to violations of its assumptions. Differences in LPE\$ between areas were partly due to differences in vessel sizes (and their associated catching power and costs) between areas, and differences in movement costs to each area. However, the examination did not unequivocally support either LPE\$ hypothesis, but instead suggested that equalization or maintenance of relative net LPE\$ might be the result of movement patterns. The examination fell short of a complete accounting of the effects of fishing costs, but it revealed the importance of including costs, when possible, in movement studies.

Some generalizations can be drawn from these three examinations of movement patterns in fisheries. First, tightly regulated fisheries, with short periods of fish availability and better information on catch rates favor greater fleet movement and numerical responses. From the fishermen's perspective, tight regulations and short periods of fish availability exacerbate the common property nature of fisheries. Fishermen are forced to make quick decisions that may affect the success of the whole season. For example, the salmon seine fishery has legal fishery openings that last only a few hours, and most salmon runs are only available in any one area for a few weeks. Thus, the seine fleet has "evolved" to include large vessels that are capable of greater movements.

Second, fisheries with year round seasons are more likely to have traditional fleet movement patterns. In these types of fisheries, there is less reliance on a particular trip to make the season profitable and therefore fishermen can work at their own pace to a greater extent than is possible in the salmon fisheries. In some cases, traditional patterns may result from low mobility and be seemingly unrelated to patterns in resource availability (e.g. Fig. 2.8, area 3). However, traditional patterns may also result from high mobility, if movement is tightly linked to consistent numerical responses and repeatable patterns of fish availability among years (e.g. Figs. 2.8 & 2.9, areas 4 & 5).

Third, costs are important considerations in movement studies. For example, including fishing costs was important in the trawl fleet because the fleet is a heterogenous group with different size vessels fishing different areas and because vessels may only land their catch at ports located at opposite ends of the province. Similarly, given that Hilborn and Ledbetter (1979) failed to reject the Maintain Relative LPE\$ hypothesis, the assumptions of equal fishing costs and negligible movement costs may have also been violated for the salmon

seine fleet, despite the fact that the fleet is more homogenous, and landing areas (in the form of small plants or mobile packing vessels) are available in every area with a major seine opening.

Data Problems and Statistical Issues

Data Problems

The three studies on different segments of B.C. fisheries have all used the same basic source of data: Department of Fisheries and Oceans saleslips. While this database contains a wealth of information, it is not ideally suited for movement studies.

For example, in examining numerical responses, all three studies chose the basic unit of one week for comparisons between effort and LPE\$. However, the saleslip data only indicate the date landed, so weeks refer to the week of reported landing. Daily catch or haul information would be better because the time scale is more similar to the time scale of information flow in the fisheries (i.e. fishermen may learn of catch rates and respond within a trip instead of only between trips). Unfortunately, accurate daily catch data are rarely available, which makes testing the affects of different levels of temporal aggregation difficult.

Determining the appropriate spatial scales for analysis is also problematic for this data set because information from saleslips is used to monitor catch quotas. When the quota is either nearly caught or completely caught, there is an incentive for skippers to misreport the location. In the case of the trawl fleet, the misreporting is probably isolated to trips involving particular species or groups (e.g. Pacific ocean perch and other rockfish), but to my knowledge the

extent of misreporting has not been evaluated. Nonetheless, researchers interested in movement studies are faced with a trade-off between selecting areas large enough to have some confidence in the accuracy of the information, but small enough to capture the movement dynamics. In the case of the trawl fishery, a more reliable data base from port sampler interviews exists, but its continued existence depends, justifiably, on the confidentiality of the information. For a general discussion of data aggregation and other problems with fisheries data sets see Gates (1984).

Statistical Issues

Even with accurate reporting, fisheries data usually present several problems that make application of the normal statistical recipes inappropriate. LPE\$ observations are not usually distributed normally (see Swierzbinski 1985 for a discussion of typical distributions). Furthermore, while several observations of LPE\$ for a given time period are often available, these usually represent different vessels with different catching power and therefore they often cannot be treated as replicates because vessel size differences may confound the ability to detect differences between areas. Thus data are usually aggregated (i.e. $\Sigma C/\Sigma E$), which leaves one observation per test cell.

One example of lack of replication is the test of the RPA hypothesis on the annual time scale. For statistical purposes, the null hypothesis is

H_0 : There is no significant difference between years in the ratio to provincial average of each area.

However, with only one observation per cell (i.e. year; Figs. 2.14, 3.4), the null hypothesis cannot be tested in the normal fashion. Therefore, previous authors

and this study have attempted indirect methods of testing the RPA hypothesis.

Hilborn & Ledbetter (1979) constructed a two-way ANOVA to test for differences in landed value per boat week where one effect was the area and the other was the year. They found very significant differences between areas and years. However, their method does not test the RPA null hypothesis because significant differences between areas and years could result even if RPA did not remain constant among years. Millington (1984) tested for differences in RPA between years by calculating rank correlations between years of the RPA's across areas. He found the correlations were not significant, which indicated the ranking of area RPA's differed between years. The Kendall's concordance measure I reported (i.e. for Figures 2.14 & 3.4) is analogous to an average of Millington's rank correlations calculated for each possible pair of years. But again the concordance measure, while quantifying the agreement in ranks of RPA between years, falls short of a true test of the null hypothesis.

General Implications

Understanding movement patterns has implications for (1) predicting the responses of fleets to changes in regulations, and (2) evaluating changes in the economic performance of fishing fleets and areas.

The primary regulatory tool that has been used to manage the British Columbia trawl fishery and other trawl fisheries is a catch quota. In recent years in the British Columbia trawl fishery, quotas for some species (e.g. various rockfishes) have been allocated on a quarterly or trip basis. While these regulatory measures are usually effective in achieving stock conservation, they often result in economic inefficiencies because more trips are required to land a

given quantity of fish and "scrambles" for shares of the quota occur more frequently.

Economists have suggested alternative regulatory tools (e.g. transferable individual vessel quotas, area licensing, royalties on landings or effort) which can in theory result in more efficient harvesting and greater net economic benefits from the resource (e.g. Moloney and Pearse 1979; Clark 1980). Implementation of these schemes will require an understanding of vessel movement patterns. For example, if a tax is to be used to shift effort among species and/or areas, understanding the potential numerical response (either positive or negative) is essential. An understanding of traditional movement patterns would be important to evaluating area licensing proposals.

The techniques applied to evaluate the movement hypotheses would be useful for examining economic measures of fleet performance on a coastwide or area specific basis. LPE\$ whether absolute or relative (i.e. Ratio to some average LPE\$) provides a much more meaningful measure of changes in the economic state of the fishery over time than the commonly used aggregate measures such as landed value of the catch, because LPE\$ measure value relative to inputs (i.e. effort). LPE\$ can also be used to compare alternative areas over time. The standardization of effort based on dollar value of the catch as suggested by Carlson (1975) and that I applied to the trawl fleet in Chapter 3, is an important step in calculating LPE\$ indices, especially for heterogenous fleets such as the trawl fleet.

Chapter 5: Literature Review of Functional Responses in Natural Predators

Introduction

Solomon (1949) defined the functional response as the relationship between the number of attacks or consumption rate of a predator, and the prey or predator density. Four forms of the functional response relating the number of attacks per predator per unit time to prey density were proposed by Holling (1959a, 1965) (Fig. 5.1). The type I response is characterized by a linear rise in the number of attacks as prey density increases followed by a plateau in attacks at higher prey densities. The number of attacks in a type II response also rises to a plateau, but the form is curvilinear with a decelerating slope. The type III response is sigmoid. The type IV response is similar to a type II response, except that the number of attacks actually decreases at high prey densities.

The remainder of this chapter is divided into three main sections. Section 1 presents equations for the four main forms of functional responses (Fig. 5.1) and a generalized equation which is able to describe all four forms depending on its parameter values. There are three primary reasons why I present the equation(s) for each functional response. First the equations provide a precise definition of each functional response. Second, it is helpful to refer to the equations when considering mechanisms for the functional response. Third, my review of functional responses in fisheries (chapter 6) will occasionally refer to these equations to draw analogies between processes in natural predation and fishing.

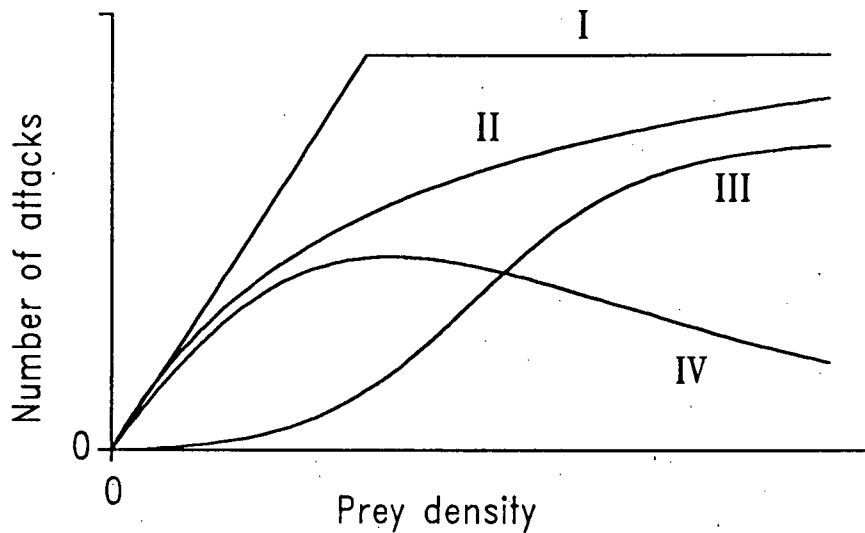


Figure 5.1. Four types of functional response curves.

Section 2 reviews the mechanisms for each type of functional response. The switching mechanism for type III responses is discussed in particular detail because it has been commonly found in natural predators and it is particularly relevant to multispecies fisheries.

Section 3 briefly considers functional responses in the context of the stability of predator-prey interactions. Only the type III response is shown to be potentially stabilizing. Chapter 6 reviews several studies that have found type II responses in fisheries; this form is potentially destabilizing to fish populations (e.g. Clark 1974).

Functional Response Equations

Type I Equations

The type I response can be described by two equations (Hassell 1976):

$$NA = aTN \text{ when } N < N_x \quad (5.1a)$$

$$NA = aTN_x \text{ when } N \geq N_x \quad (5.1b)$$

where NA is the number of prey attacked per predator, a is the rate of effective search (the area or volume searched per unit time; Holling 1965,1966), T is the time prey are exposed to the predator, N is the prey density and N_x is the threshold prey density above which the number of attacks is constant (Fig. 5.1).

Type II Equations

The most commonly used equation for the type II response is Holling's (1959b) disc equation. Holling's studies of the functional response dissected predation into its principle component processes (Holling 1959a,1961). He classified the components of predation as either basic (universal) or subsidiary (not always present). Holling's three basic components were the rate of successful search (a), the time prey were exposed to predation (T) and the time predators spent handling each prey (t_h). Subsidiary components included hunger, learning by the predator, inhibition by the prey, facilitation and interference between predators, and avoidance learning by the prey. Holling (1959b) assumed that the rate of

encounter of predators and prey is proportional to the prey density ($NA = aT_s N$) and the time spent searching ($T_s = T - t_h \times NA$). These assumptions lead to the disc equation:

$$NA = \frac{aTN}{1 + at_h N} \quad (5.2)$$

In the disc equation the rate of effective search, a , determines how fast the type II curve approaches the plateau, and the maximum number of attacks is equal to T/t_h (Fig 5.1). Note that the disc equation is algebraically identical to the Michaelis-Menten equation for enzyme kinetics (Michaelis and Menten 1913).

A second equation for the Type II response is attributed to Gause (1934 cited in Taylor 1984).

$$NA = A_{max} (1 - e^{-aN}) \quad (5.3)$$

where A_{max} is the maximum number of prey attacked per predator (i.e. the asymptote for the type II response in Fig. 5.1) and all other terms are as described above.

Type III Equations

Two main types of equations have been proposed for the type III response. Both equations hypothesize an increase in the rate of effective search with prey density in order to produce the accelerating portion of the sigmoid response (Fig. 5.1).

Hassell et al. (1977) found that the rate of effective search (a), increased with prey density in an form analogous to a type II response, for some predators that exhibited a type III functional response.

$$a = \frac{uN}{1+vN} \quad (5.4a)$$

Substituting equation 5.4a for a into the disc equation yields the type III response of Hassell et al. (1977).

$$NA = \frac{uTN^2}{1+vN+ut_hN^2} \quad (5.4b)$$

The second expression for the type III response is attributed to Murdoch and Oaten (1975) and Real (1977). Real's derivation follows directly from the disc equation. First, Real rearranged the disc equation (eq. 5.2) by dividing the numerator and denominator by aN yielding

$$NA = \frac{T}{t_h + 1/(aN)} \quad (5.5a)$$

Next, he noted that in this form the number of prey attacked, NA , is the total time available for foraging (T) divided by the total time necessary to search for, capture and handle one prey (t_h is the time spent handling each prey, and the time necessary to locate one prey (t_l) is equal to $1/(aN)$). Real hypothesized that in the type III response, t_l would be a decreasing function of the number of encounters as predators gain experience, or

$$t_l = \frac{1}{aN^n} \quad (5.5b)$$

where n is a parameter measuring the number of encounters a predator must have with prey in order to reach maximum efficiency. Substituting this expression back into equation 5.5a yields the second expression for the sigmoid response.

$$NA = \frac{aTN^n}{1 + at_h N^n} \quad (5.5c)$$

Note that equation 5.5c also assumes that a increases with prey density, because an identical equation would result if aN^{n-1} were substituted for a in the disc equation. Thus, equation 5.5c yields a sigmoid response for $n > 1$ and a type II response if $n = 1$ (Real 1977).

Type IV Equations

Tostowaryk (1972) modified the disc equation to generate a type IV response. Again the derivation starts with equation 5.2. First, note that equation 5.2 may be rewritten as

$$NA = a(T - t_h NA)N \quad (5.6a)$$

Tostowaryk observed that group defense by sawfly larvae reduced the attack rate by an Hemipteran predator at high prey densities resulting in a type IV response. To incorporate this observation into the disc equation, he hypothesized that group defense acted to increase handling times. He found that the increase in handling time was proportional to the square of the larval density and modified the disc equation as shown below:

$$NA = a(T - (t_h + cN^2)NA)N \quad (5.6b)$$

where cN^2 represents the added time needed for handling due to group defense. Solving 5.6b for NA yields an equation for a type IV response.

$$NA = \frac{aTN}{1 + at_h N + acN^3} \quad (5.6c)$$

Alternatively, various equations from nonpredator-prey literature could be adapted to describe a type IV functional response. One example, is the Ricker reproduction curve shown below (Ricker 1954, 1975).

$$R = Se^{a-bS} \quad (5.7a)$$

where R is the number of offspring and S is the number of parents. Substituting NA for R and N for S yields an expression that generates a dome shaped curve.

$$NA = Ne^{a-bN} \quad (5.7b)$$

In this form, e^a (analogous to the rate of effective search above) determines how steeply the response rises at low prey density and $1/b$ represents the prey density where the number of attacks is maximum (i.e. the prey density corresponding to the peak of the type IV curve in Fig. 5.1).

A Generalized Equation

Finally, Fujii et al. (1978) derived one equation that can produce all four functional response types. Fujii et al. follow Hassell et al. (1977) in assuming that the rate of effective search varies with prey density, but Fujii et al. use the expression shown below instead of equation 5.4a:

$$a = de^{cN} \quad (5.8a)$$

where d and c are constants. Substituting this expression for a into the disc equation (5.5a) yields Fujii et al.'s "descriptive" equation:

$$NA = \frac{T}{t_h + 1/(dN \exp(cN))} \quad (5.8b)$$

Equation 5.8b has the following properties (Fujii et al. 1978):

1. A type I response is generated when $c = d \times t_h^2$.
2. A type II response results when $c = 0$ and $t_h > 0$, or when c and $t_h > 0$ and $c < d \times t_h$.
3. A type III response occurs when $c > d \times t_h$.
4. A type IV response is produced when $c < 0$.

Thus, if equation 5.8b is fit to a given data set, the estimated parameter values can be used to judge which form of functional response best describes the data. Note, however that merely determining the "best fit" parameter set does

2 Technically, the Type I response requires two equations (i.e. eqs. 5.1 a & b), but equation 5.8b does produce a linear rise with a decelerating approach to a plateau under the conditions specified in 1.

not provide any definitive clues as to the mechanisms that are causing the observed form of the response. Also, if parameter confidence intervals are taken into account, it is likely that more than one form of functional response may be equally consistent with the data. Nevertheless, equation 5.8b provides a consistent method to test for, or model alternative functional response forms.

Instantaneous vs. Exploitation Equations

All of the equations presented thus far are based on experimental settings where prey can be replaced as they are depleted by predation. These equations are called *instantaneous* equations because they do not account for prey depletion by the predator. Instantaneous equations only apply technically to cases where either: 1. prey are replaced as they are depleted (e.g. during the course of an experiment), 2. the overall depletion of prey during the total time period of exposure is small, or 3. predators search systematically (i.e. they do not return to previously depleted areas; Rogers 1972; Hassel et al. 1976). Thus, instantaneous equations apply to cases that are unaffected by "diminishing returns" (Royama 1971).

To be of some value in modeling predator-prey systems, these instantaneous equations must be incorporated into *exploitation* equations. Exploitation models of predation account for prey depletion by integrating over the time during which prey depletion occurs (Royama 1971). The general form for the rate of change in prey density (dN/dt ; for the case of depletion by predation only) is given by

$$\frac{dN}{dt} = -NAP \quad (5.9)$$

where NA is the instantaneous functional response equation, and P is the number of predators (Royama 1971). The exploitation equation is determined by first integrating equation 5.9 between the limits $N=N_0$ (the initial prey density) and $N=N_0-NE$, and $t=0$ and $t=T$, and then solving the result for NE (the number eaten taking into account prey depletion; Royama 1971; Fujii et al. 1978). For the disc equation (eq. 5.2), the resulting exploitation equation is

$$NE = N_0(1 - e^{-a(PT - t_h NE)}) \quad (5.10)$$

where the symbols are as in equation 5.2 and NE and P are defined above.

Equations 5.9 and 5.10 assume that predators do not interfere with each other. For more complicated exploitation models that account for interference see Beddington (1975) and Royama (1971). Equations for the other functional response forms can be derived in the same fashion. However for type III responses, exploitation equations can be quite complicated (e.g. eq. 36; Fujii et al. 1978). Exploitation equations are appropriate for use in population models to determine deaths due to predation.

The next section considers some properties of predators and their prey that have been proposed as mechanisms for the four types of functional responses.

Functional Response Mechanisms

In his original work, Holling (1959a, 1965) found type III responses by small mammals predators to the density of pine sawfly cocoons, and a type II response by preying mantis to the density of fly adults or larvae. Other authors

have since found all four forms in a variety of vertebrate and invertebrate predators (See Murdoch and Oaten 1975, Fujii et al. 1978, and Taylor 1984 for reviews). These studies and those of Holling (1959a&b, 1965, 1966) proposed various mechanisms that could lead to the four types of functional responses that have been documented.

Type I and II Mechanisms

First, the plateaus in response types I-III, and the peak in type IV, result from limited time available for foraging relative to handling (i.e. T and t_h in above equations 5.1a & b, 5.2, 5.4b, 5.5c, 5.6c and 5.8b) and/or satiation of the predator (Holling 1965). The type I response results if a predator has a constant time spent searching until satiation (Taylor 1984), and this form has been found for some filter feeding zooplankton species (Murdoch and Oaten 1975).

Two mechanisms are commonly proposed for the type II response (reviewed in Taylor 1984). The first mechanism is a continuous decrease in searching rate or percent of time spent searching as the gut is filled, arising primarily from the effects of hunger upon the motivation to hunt (Gause 1934 and Ivlev 1961, cited in Taylor 1984; resulting in equation 5.3). The second mechanism is a reduction in searching time available due an increased proportion of the total time spent handling as prey density increases (Holling 1959b; resulting in the disc equation, 5.2). It is likely that both mechanisms operate in many cases. These two mechanisms also cause the type III response to decelerate to an asymptote.

Type III Mechanisms

The two previous sections have discussed the mechanisms for the deceleration and asymptote of the type III response. The underlying cause for the accelerating portion of the type III response is an increase in the rate of effective search (a) as prey density increases from low to intermediate levels (Holling 1965; Murdoch and Oaten 1975; e.g. via equations 5.4a or 5.5b). Several mechanisms have been proposed that could result in increased search rate and/or efficiency.

Alternative mechanisms for type III functional responses were reviewed by Murdoch and Oaten (1975). They considered that the form of the functional response was not only determined by the behavioral options available to the predator, but also the characteristics of the prey (e.g. density, distribution in space and time). Murdoch and Oaten (1975) outlined three principle mechanisms for the type III response.

1. The predator is stimulated to spend a greater proportion of time hunting and/or hunting efficiency increases through learning when prey abundance increases.
2. The prey occur in patches of different densities and the predators feed more often in the high density patches and/or a limited number of spatial prey refugia are available and prey in refugia are less vulnerable to attack.
3. Switching by the predator between less abundant and more abundant prey (by various mechanisms, see below).

Studies of parasite-host systems (analogous to predator-prey systems in many respects) have found that parasites may be stimulated to spend an increasing proportion of their time hunting as host density increases (Burnett 1964, Takahashi 1968). However most examples of mechanism 1 operating in predator-prey systems have involved some form of predator learning. In fact, predator learning was the first mechanism suggested for the type III response (Tinbergen 1960, Holling 1965). Tinbergen's (1960) concept of a predator search image is one example of predator learning that dominated the early literature on Type III functional response mechanisms.

Tinbergen (1960) observed a sigmoid relationship between the *proportion* of a given prey species (caterpillars) in the diet and the density of the same species available to the predator (great tits); a straight line relationship would be expected from random search (Fig. 5.2). To explain this observation, Tinbergen suggested that the birds learned to concentrate on certain characteristics of the prey (size, shape, color, etc.), and he called this learned response the development of a specific searching image. Thus, when species *i* was abundant, birds focused on species *i* and overlooked less abundant prey resulting in a diet with larger proportions of species *i* (Fig. 5.2). When the abundance of species *i* decreased, Tinbergen hypothesized that the birds abandoned their specific search image for species *i* and acquired a search image for a more abundant prey type resulting in lower proportions of species *i* in the diet than expected from random search. The plateau in the curve at high densities was attributed to the need for a varied diet (Fig. 5.2).

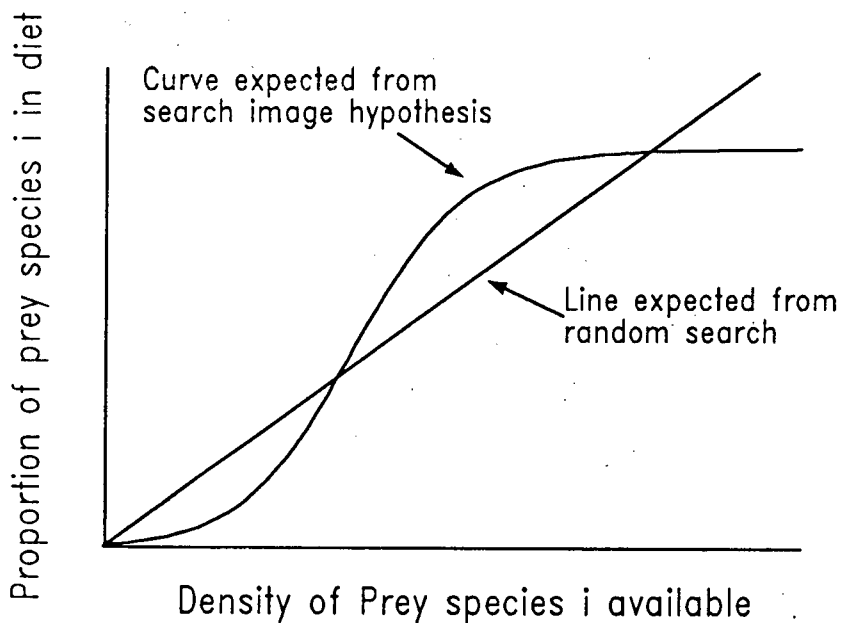


Figure 5.2. Tinbergen's (1960) search image hypothesis (from Hassell 1976).

Holling (1965) saw analogies between his work with small mammal predators feeding on sawfly cocoons and Tinbergen's work on birds. Holling (1959a, 1965) observed a type III functional response and suggested that one logical component of predation that could result in the accelerating portion of the response was a predator learning to associate stimuli with the prey. He supported this hypothesis with experiments in which naive predators were exposed to a constant density of prey, and he found that the attack rate increased with the time predators were exposed to the prey. He also found an extinction of the learning response (i.e. forgetting). Next, he developed a simulation model that included learning, and it generated a type III response. Despite the fact the predator was provided with an alternate food, he did not suggest a strict search image explanation for his observations, perhaps because the alternate food (dog biscuits) was rather unpalatable in comparison to the sawfly cocoons.

While the ability of predators to develop visual cues for and learn to associate stimuli with particular prey has not been questioned, the idea of search image formation and learning as the likely mechanisms for Tinbergen's and Holling's observations has been criticized.

Murdoch and Oaten (1975) extensively reviewed Tinbergen's search image hypothesis and concluded that it had been subject to misinterpretation in the literature. Below are two major points of clarification they provided concerning the search image hypothesis:

1. A sigmoid relationship between the proportion of prey in the diet and the abundance available does not necessarily imply compensatory mortality on the given prey during the accelerating part of the curve (i.e. does not imply a type III functional response). Inferences concerning the shape of the functional response can be drawn from these plots only if the absolute predation rate is provided or the total number of all prey species in the diet is constant.
2. Tinbergen's verbal account of the search image hypothesis, and subsequent analysis by Mook et al. (1960), actually suggest that search image formation implies a change in behavior in time, as well as, or instead of with prey density. Therefore, to test the hypothesis, it is necessary to look at attack rates through time. Conditions where the development of a search image will lead to a type III functional response are reviewed further in Murdoch et al. (1975).

Critics of Tinbergen's (1960) search image hypothesis and Holling's (1965) learning explanation have suggested that both authors' observations could be better explained by mechanisms 2 and 3. These mechanisms are reviewed in the

next two sections.

Prey Patchiness or Prey Refugia

Mechanism 2 is presumably widespread among predators (Murdoch and Oaten 1975) and it has been modeled by Hassell and May (1974). Royama (1970) first suggested mechanism 2 as an alternative explanation for Tinbergen's (1960) observations. Royama (1970) showed that if the proportion of time a predator spends in patches containing a given prey type increases as the density of that prey type within patches increased, the proportion of prey types in the diet would vary relative to the absolute number available in a manner consistent with the search image hypothesis. Furthermore, Royama's explanation results in a type III functional response and it does not require any learning on the part of the predator. When two or more prey types are involved, Royama's mechanism may result in the observations consistent with switching (see below).

The Switching Mechanism

In addition to clarifying Tinbergen's search image hypothesis, Murdoch and Oaten (1975) suggested an alternative explanation to learning for Holling's (1959a,1965) observed type III functional response in deer mice. They suggested that the observations could be explained if the mice tended to concentrate on the feeding pattern that was more rewarding. Since cocoons were preferred to dog biscuits, the reinforcement from a cocoon meal should be greater than for a dog biscuit meal and so they expected searching would persist for cocoons even when cocoons were rare. However, when cocoons were sufficiently rare, Murdoch and

Oaten hypothesized that the mouse switched to biscuits. A similar mechanism has been proposed for predation by guppies (Murdoch et al. 1975).

Taylor (1984) proposed a similar alternative to Holling's learning hypothesis, except Taylor suggested that if cocoon density was sufficiently low, the deer mice might simply choose not to search for cocoons and dig them out of the sand, because the activity was unprofitable. Thus, Taylor suggested that an increase in time spent searching (relative to the total time exposed) by mice as cocoon density increased would result in a type III response.

This "switching off" mechanism of Taylor (1984) has been proposed for a variety of zooplankton species (e.g. Adams and Steele 1966; Parsons et al. 1969; Steele and Henderson 1977).

Murdoch and Oaten (1975) also compared the search image hypothesis to the switching hypothesis (Murdoch 1969). This comparison is briefly summarized in the next section.

The Switching Hypothesis

The switching hypothesis relates the proportion of two prey types in the diet to the proportion of the types available (Murdoch 1969). This hypothesis is distinct from the search image hypothesis that relates the proportion of a prey item in the diet to the item's absolute density available (Murdoch and Oaten 1975; cf. Figs. 5.2 and 5.3b). Murdoch (1969) defined switching in the case of two prey as a changing preference such that the ratio of two prey types in the diet would increase at a rate disproportionate to the change in their relative availability. He

defined the null case (no switching) by the equation

$$\frac{D_1}{D_2} = c \frac{N_1}{N_2} \quad (5.11)$$

where D_1 and D_2 are the numbers of prey types 1 and 2 in the diet and N_1 and N_2 are the numbers available to the predator. The parameter c is a constant that measures preference, such that when $c=1$ prey types have equal preference, when $c<1$ prey type 2 is preferred and vice versa for $c>1$ (Murdoch 1969). Thus, the switching hypothesis defines preference as the ratio of the numbers of two prey types in the diet when equal numbers of the each prey type are available to the predator. Note that D is the same as NA in the functional response equations, and c is a_1/a_2 (see below).

In the absence of switching, c is expected to be constant, and the relationship expressed in equation 5.11 would be a straight line (Fig. 5.3 A; Murdoch 1969, Murdoch et al. 1975). If switching occurs, the ratio of prey items in the diet should increase faster than linearly as the ratio of prey items available increases (i.e. c is an increasing function of N_1/N_2 ; Fig 5.3 A).

The switching model is often expressed in terms of the proportion of a prey item in the diet (i.e. $D_1/(D_1+D_2)$) relative to the proportion of that prey item available (i.e. $N_1/(N_1+N_2)$). When expressed in this way, the null hypothesis is still a straight line and the curve for switching is sigmoid (Fig. 5.3 B; see Murdoch and Oaten 1975).

Several studies have tested the switching hypothesis, and the principal conclusions from the tests were summarized by Murdoch and Oaten (1975; also see Murdoch et al. 1975). Generally, studies failed to reject the null hypothesis (i.e. no switching) under two conditions: either when preference at equality (i.e.

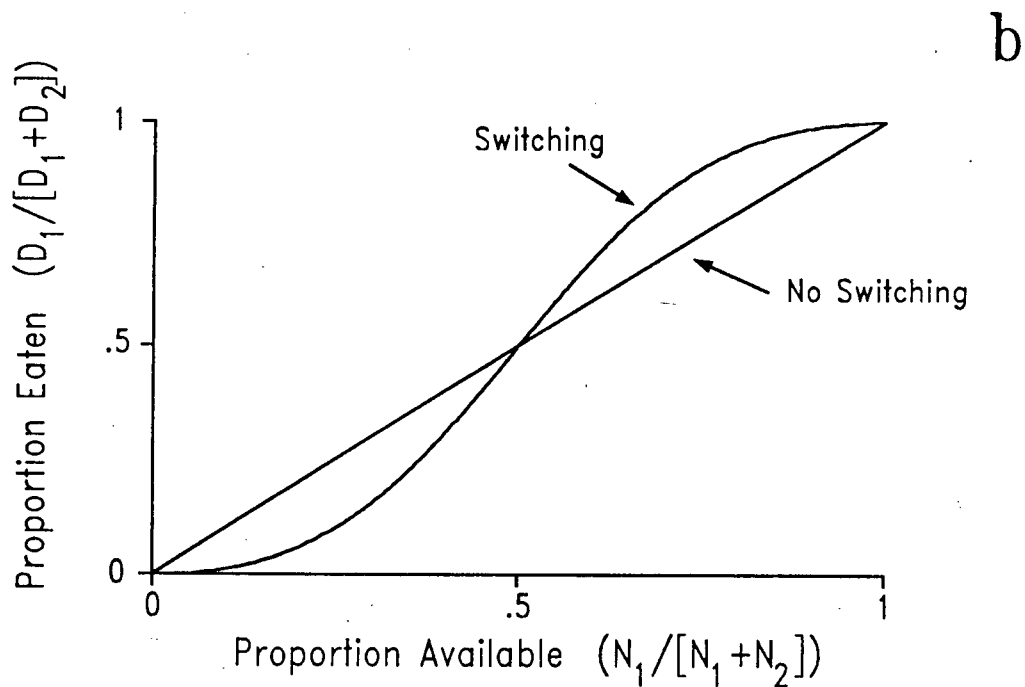
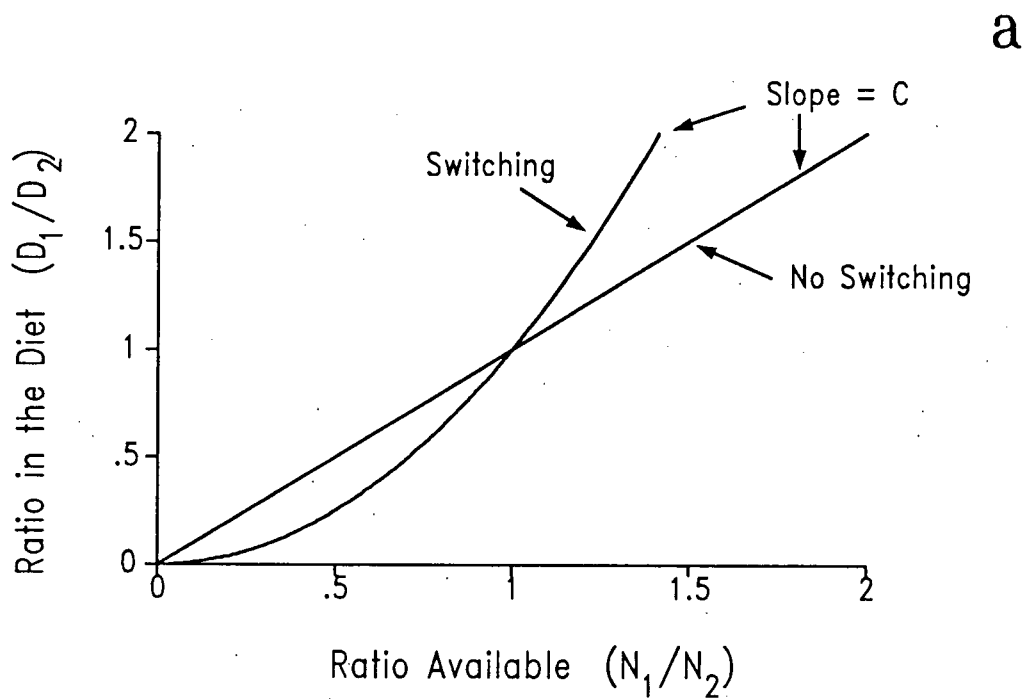


Figure 5.3. A. Switching hypothesis expressed as ratios. Switching curve was drawn using equation 5.16 with $\lambda_1/\lambda_2 = 1$. **B.** Switching hypothesis expressed as proportions. Switching curve was drawn using equation 27 in Murdoch and Oaten (1975; p. 62).

when $N_1 = N_2$) was consistently strong (i.e. $c \gg 1$) or consistently weak among individual predators (i.e. $c \ll 1$). Switching was found in cases when preference at equality was weak (i.e. $c \ll 1$) averaged over all predators, but strong and highly variable among individuals.

Mechanisms for Switching

Various mechanisms have been proposed to explain the occurrence of switching. Murdoch et al. (1975) listed four common mechanisms:

1. Prey types are found in different areas, and predator spends longer in an area as the relative reward rate there increases.
2. Rate of detection or recognition depends on recent experience.
3. Rate of acceptance/rejection of each species depends on recent experience.
4. Rate of successful attacks on each species depends on recent experience.

Examples of studies that attributed switching to each of the above mechanisms were presented in Murdoch et al. (1975) and Murdoch (1977). "Flocking" (i.e. individual predator diets influenced by those of predators near them) was suggested as a switching mechanism by Murdoch and Oaten (1975).

Switching and the Functional Response

In order to include switching in functional response models, it was necessary to extend the models to include more than one species. Murdoch (1973)

generalized Holling's disc equation to k prey species as shown below.

$$NA_j = \frac{a_j N_j T}{1 + \sum_i a_i t_{hi} N_i} \quad (5.12)$$

where all symbols are the same as in equation 5.2 and the subscripts refer to prey species. Equation 5.12 is called the multispecies disc equation (MSDE). Murdoch and Oaten (1975) show that if the MSDE is expressed for two prey species, (as in equations 5.13a & b below) and the equation for the attack rate on one prey is divided by the attack rate for the other, the result is the switching null hypothesis (equation 5.14 below):

$$NA_1 = \frac{a_1 N_1 T}{1 + a_1 t_{h1} N_1 + a_2 t_{h2} N_2} \quad (5.13a)$$

$$NA_2 = \frac{a_2 N_2 T}{1 + a_1 t_{h1} N_1 + a_2 t_{h2} N_2} \quad (5.13b)$$

$$\frac{NA_1}{NA_2} = \frac{a_1}{a_2} \frac{N_1}{N_2} \quad (5.14)$$

where NA and a_1/a_2 are equivalent to D and c of equation 5.11. Murdoch and Oaten (1975) incorporated switching into the MSDE, by assuming the rate of effective search for each prey species increased linearly with the proportion of the species available. They let $a_i = \lambda_i P_i$ where $P_i = N_i/(N_1 + N_2)$ (Note: in their notation, $\lambda_i = a_i P_i$ because they used λ_i to denote the rate of effective search). With these substitutions, the functional response model for switching in the two prey case is

$$NA_i = \frac{\lambda_i P_i N_i T}{1 + \lambda_1 t_{h1} P_1 N_1 + \lambda_2 t_{h2} P_2 N_2} \quad (5.15)$$

Equation 5.15 results in a switching hypothesis of

$$\frac{NA_1}{NA_2} = \frac{\lambda_1}{\lambda_2} \frac{N_1^2}{N_2^2} \quad (5.16)$$

Note that the ratio of the two prey items in the diet (i.e. NA_1/NA_2) increases faster than linearly with the ratio available, as expected if switching occurs (e.g. Fig. 5.3a). For a more detailed method of including switching in the functional response see Oaten and Murdoch (1975b).

The MSDE will generally result in a type II response for both prey species (Murdoch 1973; Murdoch and Oaten 1975). When switching is included (as in eq. 5.16), a type III response results for both prey species if handling times are equal among prey species and the total density is fixed, but in general a type III response occurs in one species (often the preferred prey; Murdoch and Oaten 1975).

In summary, when the diet of the predator is composed of more than one prey species, various mechanisms may result in switching in the predator. When switching occurs, it is a common mechanism for the type III response. However, the occurrence of switching does not necessarily lead to a type III response. The generation of a type III response depends on the extent to which increases in the rate of effective search due to switching (that causes an acceleration in the response) are counteracted by increased total handling time (that causes the response to decelerate).

Type IV mechanisms

Holling (1965) found that when he included learning in his simulation model of the vertebrate functional response, a type IV response sometimes resulted for distasteful prey. He thought that this response could result in the field if predators developed specific *nonsearch* images (i.e. the reverse of Tinbergen's 1960 concept). Subsequent studies have attributed type IV responses to three main mechanisms: predator confusion, predator disturbance by prey, and group defense in the prey. The group defense mechanism was proposed by Tostowaryk (1972) and is included in the functional response equation 5.6c above. Confusion of the predator was first proposed by Welty (1934). He found that several *Daphnia* present in the immediate field of vision of a goldfish offered conflicting stimuli that blocked the feeding response. Mori and Chant (1966) documented the disturbance mechanism. They found that a predacious mite was disturbed by contacts with other prey at high prey density, and would consequently abandon attacks. For other examples of type IV responses see Fujii et al. (1978).

Functional Responses and Stability

Much of predator-prey literature concerns the ability of predators to stabilize prey populations. Thus, many investigations of functional responses have commented on the implications of the form of the functional response for stability (e.g. Holling 1965; Murdoch and Oaten 1975; Oaten and Murdoch 1975a, b; Hassell 1978; Taylor 1984; Kuno 1987). Oaten and Murdoch (1975a) pointed out the importance in defining stability because of the various types of stability that

exist in mathematical models and the difficulty in defining stability in real communities. Holling (1965) and Murdoch and Oaten (1975) others have emphasized that it is actually the form of the total response (functional and numerical) that is relevant to stability. With these caveats, and for the purposes of this brief summary, I will define stability as damped fluctuations about some average ("equilibrium") value and consider which forms of the functional response can be potentially stabilizing to prey populations.

Holling (1965) stated that a functional response could be stabilizing if the number of attacks resulted in increased percent mortality as prey density increased. To determine which functional responses cause compensatory mortality, the equations are expressed as percent mortality for each type (Fig. 5.4). Thus, only the type III response can potentially stabilize prey populations. Types I, II and IV are potentially destabilizing, particularly if the prey have a depensatory reproduction curve (e.g. Clark 1974).

Oaten and Murdoch (1975a) considered two measures of the stabilizing effect of functional responses. First, they considered whether the response causes compensatory mortality, which occurs when

$$f'(N) > f(N)/N \quad (5.17)$$

where $f'(N)$ is the first derivative of the functional response equation ($f(N)$) with respect to prey density (N). Equation 5.17 holds when an increase or decrease in the prey population results in a greater than proportionate increase or decrease in predation by a single predator. Their first measure of the stabilizing effect was the range of prey abundances (N_m) over which compensatory mortality occurs. The second measure was $f(N_m)$ that provides a measure of the range of parameter values for a given predator prey model over which the functional

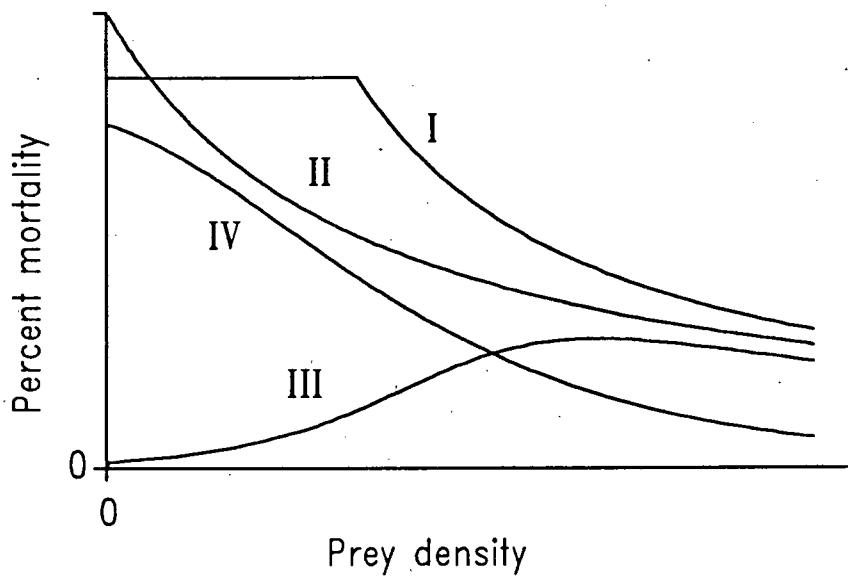


Figure 5.4. Percent mortality curves for the four types of functional responses shown in Figure 5.1. Only the type III response, results in compensatory mortality over a range of prey densities and is potentially stabilizing.

response will yield stability (see Oaten and Murdoch 1975 a,b; Levin 1977; and Oaten and Murdoch 1977 for more detail). Oaten and Murdoch (1975b) examined the implications of switching for stability. They concluded that switching is not always stabilizing, because switching does not always result in a type III functional response.

For an examination of the implications of incorporating functional responses into various predator-prey models see Bazykin (1974), and Kuno (1987). For an analysis of fisheries stability implications see Jones and Walters (1976) and Walters (1986).

Chapter 6: Functional Responses and the Fishery

Introduction

Fishing activities include most processes found in animal predation (e.g. search, pursuit, handling and capture), yet it was not until this decade that the functional response concepts of Holling (1959a and b, 1965) were first applied to a fishery (Bienssen 1979, Peterman 1980)³. The relatively recent application of Holling's ideas to fisheries is especially surprising given that fisheries analysts and managers commonly assume that the catch per unit of fishing effort (CPUE; i.e. the number attacked per predator (vessel) per unit time) is proportional to abundance (i.e. a type I response) and the alternative forms of the functional responses have very different implications for the relationship between CPUE and abundance (e.g. Fig. 5.1).

One factor contributing to the late application of Holling's ideas to fisheries is that fishing effort data are seldom collected or reported in terms of their components. A common effort measure is days fished without mention of the hours per day spent travelling, searching, capturing, and handling, even when some of these time components are recorded in fishermen's logbooks. Furthermore, it is usually recommended that the best component of effort for use in CPUE indices is the amount of time the gear is actually fishing (e.g. hours trawling; Gulland 1955; Beverton and Holt 1957), therefore it has generally been

³ Peterman's study was the first to formally apply Holling's concepts, however the recognition that fishing effort consisted of various components occurred much earlier (e.g. Gulland 1955; Beverton and Holt 1957), and Paloheimo and Dickie (1964) were the first to propose a catch equation of type II form, but they did not recognize its relationship to Holling's work and they were unable to find suitable data sets for its application. Bienssen also apparently independently derived Holling's disc equation and applied it to an Australian abalone fishery.

considered unnecessary to examine the other components. In fact, most studies to date have simply hypothesized how the components of fishing effort might vary given an "observed" form of the functional response.

Despite the relatively recent application of functional responses to fisheries, many studies have recognized the potential biases in CPUE as an index of abundance that result from measures of fishing effort that either aggregate all components (e.g. days fished) or include only one component (e.g. hours trawled; e.g. Gulland 1964; Garrod 1964; Paloheimo and Dickie 1964; Radovich 1976).

It is important to note that while CPUE is commonly used to mean catch per unit of fishing effort, the use of LPUE or LPE (i.e. landings per unit of effort) is more accurate because in many fisheries a portion of the catch is discarded at sea. In this review, I use the abbreviation used by the cited authors, but in Chapters 7 and 8, I use LPE, since unknown quantities of groundfish are discarded by the trawl fleet. The next sections consider the functional response models of fisheries, their assumptions, and the consequences of violations of the assumptions in more detail.

Section 1 discusses the type I functional response and its assumptions in the fisheries context. The assumption of a type I response (with a very high limit on attack rate) is implicit in most theories of fish population dynamics. Section 2 reviews some studies that have questioned validity of assuming a type I functional response, many of which have provided evidence for type II responses in fisheries for a variety of fishes. Section 2 also reviews potential mechanisms for type II responses in fisheries and the management consequences of incorrectly assuming a type I response when the true response is of type II form. Sections 3 and 4 consider the possibility of and potential mechanisms for

type III and type IV responses in fisheries.

Type I Responses

Most fisheries models assume a type I functional response. This assumption is expressed in the *Catch Equation*

$$C_t = qf_t \bar{N}_t \quad (6.1)$$

where C is the number of fish caught in year t , f is the fishing effort (e.g. number of vessel-hours trawling), \bar{N} is the average number of fish available, and q , the catchability coefficient, is defined as the proportion of the population caught by one unit of fishing effort (Baranov 1918; Ricker 1940). Equation 6.1 states that CPUE (C/f) is proportional to the average abundance \bar{N} where q is the proportionality constant. The term average abundance is used because fishing and natural mortality will deplete the population over the course of a fishing season. Ricker (1944) showed that \bar{N}_t is related to the initial abundance at the start of the season (N_0) by

$$\bar{N}_t = N_0(1 - e^{-Z_t})/Z_t \quad (6.2)$$

where Z_t is the total instantaneous mortality rate and e is the base of natural logarithms ($Z_t = -\ln(\text{total annual survival rate})$). Note that Z_t may be expressed as the sum of the instantaneous rates of fishing mortality (F_t) and natural mortality (M_t ; i.e. $Z_t = F_t + M_t$) and that fishing mortality is given by $F_t = qf_t$.

An alternative expression for the catch equation due to Palohiemö

and Dickie (1964) is:

$$C_t = q'f_tD_t \quad (6.3)$$

where D_t is the average density of fish at time t (i.e. \bar{N}_t/A , where A is the total area occupied by the population), and $q' = ca$. In this form c is a parameter that measures the efficiency of the gear over the area a swept by one unit of gear for a fixed time period (e.g. by a trawl net over one standard fishing period). The two forms of the catch equation (i.e. eqs. 6.1 & 6.3) are equivalent if the area of the stock (A) remains constant at all levels of abundance.

Thus, the catch equation describes a type I response as depicted in Figure 6.1 A and it implies a constant percent mortality per predator (i.e. constant catchability coefficient) at all levels of fish population density (Fig. 6.1 B). Note that the catch equation only predicts the solid lines of Figures 6.1 A & B, but in practice it is recognized that at high levels of abundance CPUE may level off and percent mortality may decline as indicated by the dotted lines. Gear saturation, limited hold capacities and boat limits imposed by fish processing plants are among the mechanisms that have been proposed for this leveling of catch rate at high abundance levels (Radovich 1976; Rothschild 1977).

The principal assumptions of the catch equation as given in Ricker (1940) and summarized in Paloheimo and Dickie (1964) are:

1. Effort units, f , operate independently and do not compete with each other.
2. Catchability (q) is constant.

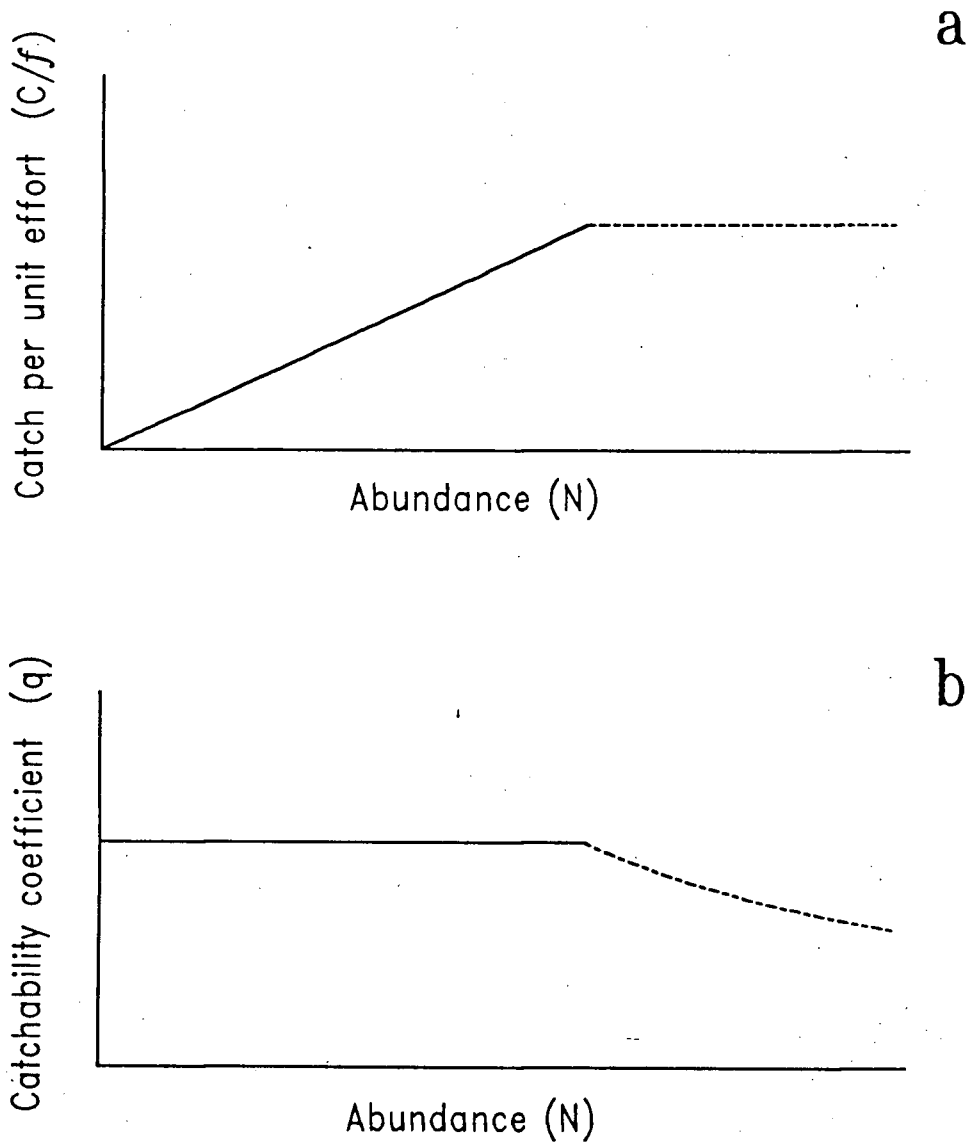


Figure 6.1. Type I functional response (A) and mortality (B) curves for the fishery. Solid lines are predicted by equation 6.1. Dashed lines are not predicted by equation 6.1, but are believed to be part of type I responses in fisheries.

Violations of assumption 1 are undoubtedly related to the level of abundance as well as the level of effort. Radovich (1976) found there was a greater reliance of vessels on communication with other vessels (i.e. less independence) when abundance was low in the California sardine purse seine

fishery. In principle, it would be possible to measure the added benefit of cooperation by comparing the CPUE of vessels fishing independently and cooperatively on similar densities of fish. However, in practice these experimental comparisons would be very difficult to set up (see Paloheimo and Dickie 1964 and Rothschild 1977 for theoretical models of cooperation).

The second part of assumption 1 concerns competition. Rothschild (1977) identified two types of competition: competition among vessels for fish (interference) and competition among fish for space in or on the gear (saturation). As with cooperation, if the extent of interference could be measured, CPUE indices could be adjusted accordingly. However, an alternative model that includes interference would be more appropriate (e.g. Watt 1959; Rogers and Hassell 1974; Beddington 1975; Rothschild 1977). The effects of saturation depend on the length of time the gear is fished. If catch and effort data are available for subperiods, the choice of short time periods should minimize the effect of saturation. However, if saturation is continuous (i.e. mimicing satiation), a type II response is more appropriate (e.g. Gulland 1955; Rothschild 1977).

Fishery scientists have recognized that many factors affect the catchability coefficient. Gulland (1955) listed four factors:

1. the fishing power of a vessel for a type of fish.
2. the vulnerability of that type of fish.
3. the aggregation of fishing units on the fish.
4. the concentration of fishing units on the fish.

Obviously, it is an impossible task to control for all these factors that affect catchability. Thus, in practice, attempts to meet the constant catchability assumption have usually centered on careful selection of the effort units (i.e. f)

such that effort is proportional to fishing mortality (i.e. $F=qr$). Garrod (1964) and Gulland (1964) have reviewed the problem of determining effective fishing effort (see also Robson 1966).

Changes in fishing power usually act to increase catchability over time. Effort standardization (e.g. Gulland 1956a) may be used to account for catchability changes that result from changes in fishing power.

Vulnerability refers to the degree to which fish are exposed and susceptible to the fishing gear. Exposure varies with the temporal and spatial distribution of fish in relation to fishing. Susceptibility depends on physical and behavioral characteristics of the fish in relation to the gear (e.g. the girth of a fish in relation to the mesh size of a gillnet). Vulnerability is usually quantified in terms of relative catchability. For example, the vulnerability of fish of various ages may be expressed as the ratio of the catchability of fish at each age to the catchability of fish at a reference age.

Vulnerability changes resulting from physical changes in the gear that directly affect susceptibility (e.g. changes in mesh size) may be accounted for by procedures analogous to effort standardization. However, changes in the vulnerability of fish resulting from changes in exposure often result in seasonal changes in catchability (e.g. Garrod 1964). Accounting for seasonal changes in exposure of a population is only possible under certain circumstances (see below).

Changes in exposure may result from changes in the level of aggregation and concentration. Gulland (1955) defined the aggregation of fishing effort as the ratio of the density of fish in the immediate area of the gear to the average density in the general area where the gear is working. He defined concentration of fishing effort as the ratio of the average density in this general area to the

average density of the whole accessible stock. Changes in aggregation or concentration of effort may cause both annual and seasonal variations in catchability.

If cyclical or seasonal variation in vulnerability is similar between years, changes in seasonal effort patterns (i.e. concentration and aggregation) may be accounted for by taking a weighted average CPUE among subperiods and/or subareas where the weights are the sizes of the subareas and the durations of the subperiods (Gulland 1955; 1964). However, if seasonal variations in vulnerability differ among years, Garrod (1964) suggested using the CPUE from a subperiod(s) during which the average catchability is constant or nearly constant among years.

Given the many factors that affect catchability, it is relevant to consider the general conditions necessary to meet the constant catchability assumption. Paloheimo and Dickie (1964) reviewed intuitive models for the distributions of fish and fishermen that would meet the constant catchability assumption. Baranov's (1918) intuitive model was a population of immobile fish that was uniformly distributed over its range. Areas fished by each vessel were of areas fished during previous sets (e.g. trawls) and independent of areas fished by other vessels. Ricker's (1940) intuitive model included a very mobile fish population that quickly repopulated locally depleted areas. Under such circumstances, the conditions for uniform exploitation and independence of effort would be met even with stationary gear as long as the gear did not directly compete or affect fish redistribution. Alternatively, Ricker hypothesized that if mobile vessels were widely dispersed over an area occupied by a moderately mobile fish population, average catchability determined from non-uniformly and uniformly distributed populations would be nearly the same. These intuitive models clearly appeared to be special

cases, and therefore Paloheimo and Dickie (1964) examined the implications of fish distribution in more detail.

As an alternative to the assumption of uniform distribution of fish, they proposed that fish were distributed in clumps or schools of a uniform size. Next, they derived an alternative catch equation based on the division of fishing effort into fishing time (time spent actually capturing a school) and time spent searching for a school. Their alternative catch equation was

$$C = \frac{2gDrt}{1+2Dr\tau/n} \quad (6.4)$$

where C is the catch, g is the proportion of fish in a school of radius r that are caught, D is the overall density of fish in the whole area containing n schools, τ is the time required to exploit a school, and t is the total operation time spent both exploiting and searching.

Next, Paloheimo and Dickie (1964) compared their catch equation (i.e. eq. 6.4) with the classical equation (i.e. eq. 6.3). They concluded that CPUE indices based on C/f (i.e. catch per fishing time) would be misleading if they were applied to fisheries that involved search for clumps or schools of fish. In such cases the apparent catchability coefficient may be expected to be inversely proportional to the overall density. Paloheimo and Dickie (1964) suggested catch per operation time as an alternative to catch per unit fishing time. However, the authors stated that understanding this alternative index would depend on knowledge of the size of schools and the density within schools as well as the overall density, and detailed information on school characteristics is rarely available.

In summary, the applicability of the type I functional response model to fisheries is highly dependent on the degree to which the model assumptions fit the data. The constant catchability assumption can be met in some cases by careful selection of the effort measure. However, some assumptions cannot be accounted for by standardization the components of the type I response, but may be accounted for in alternative models. The next section considers the type II response.

Type II Responses

Paloheimo and Dickie (1964) provided a theoretical basis for a type II functional response by fishermen. Although it was not recognized by the authors, Paloheimo and Dickie's model (eq. 6.4) is identical to Holling's 1959b disc equation (eq. 5.2) with $a = 2rg$, $T=t$, and $t_h = \tau/gn$. Paloheimo and Dickie clearly demonstrated the implications of a type II response for CPUE as an index of abundance. The most important implications are that CPUE will not be proportional to abundance and the apparent catchability coefficient (q) will be inversely related to abundance.

A study by Beinssen (1979) is a second example of a fisheries researcher apparently independently (he cites neither Holling nor Paloheimo and Dickie) deriving an expression equivalent to the disc equation. Beinssen (1979) modeled CPUE of divers harvesting abalone off the SW coast of Australia. He observed that total diving time (T) was comprised of search time (S) and handling time (H) and he postulated that total handling time was proportional to the number of abalone caught (i.e. $H = hC$; where h , the average time spent handling each abalone, is equivalent to t_h in the disc equation; eq. 5.2). Next, he hypothesized

that catch per unit of searching time rather than catch per unit of total diving time should be proportional to the density of abalone (D), because searching time was directly related to the process of locating abalone. Thus, he assumed that

$$C/S = rD \quad (6.5)$$

where the parameter r , defined as fishing power, has units of area covered per time spent searching, and is equivalent to the rate of effective search a in the disc equation (eq. 5.2). Substituting $T-hC$ for S in equation 6.5 yields

$$C/(T-hC) = rD \quad (6.6)$$

Unlike Paloheimo and Dickie (1964), Beinssen (1979) was able to estimate the parameters (r, h) for his model by using data from three separate experiments where he had mark-recapture estimates of D , and estimates of T and C for research divers. He rearranged equation 6.6 to yield

$$T/C = h + 1/(rD) \quad (6.7)$$

and estimated h (5.1 seconds per abalone) and r (1196 m^2 per hour spent searching) by regression.

Note that equation 6.6 can also be rearranged to yield

$$C = \frac{rTD}{1+rhD} \quad (6.8)$$

which is identical to the disc equation (eq. 5.2) with $a=r$ and $t_h=h$. Thus, Beinssen (1979) demonstrated that a type II functional response equation can

result from a type I functional response equation (i.e. eq. 6.3) in fisheries which meet the following three conditions: 1. total fishing time is comprised of time spent handling and time spent searching, 2. catch per unit search time rather than catch per unit total time is proportional to density, and 3. total handling time is proportional to total numbers caught.

The potential management consequences of assuming a type I response when the true response is type II were outlined by MacCall (1976) and Ulltang (1976,1980). The first consequence of incorrectly assuming a type I response is that the manager will underestimate the decline in the population, particularly at low abundance levels (i.e. $N_{II} < N_I$, Fig. 6.2 A). The situation is further exacerbated by the second consequence, which is underestimation of the fishing mortality caused by one unit of fishing effort (i.e. the catchability coefficient) at low stock sizes (i.e. $q_{II} > q_I$, Fig. 6.2 B). Thus, the manager will be overly optimistic and will be less likely to take the stringent measures (i.e. reductions in effort or allowable catches) that may be required to prevent overfishing (e.g. MacCall 1976; Ulltang 1976; Sinclair et al. 1985). The extent that managers may be misled depends on the degree of nonlinearity in the type II response. Under certain conditions, a type II response may lead to stock collapse (e.g. Clark 1974). See also Fox (1974) and Condrey (1984) for the implications of density dependent catchability for surplus production models (i.e. logistic models).

The first evidence for type II responses in fisheries appeared about ten years after Paloheimo and Dickie's (1964) original model. One misconception about Paloheimo and Dickie's model was that knowledge of the size of schools and density of fish within schools was required in order to test the model empirically. Thus, the delay may have been due to an inability of researchers to view some of Paloheimo and Dickie's rarely measured components (e.g. school size

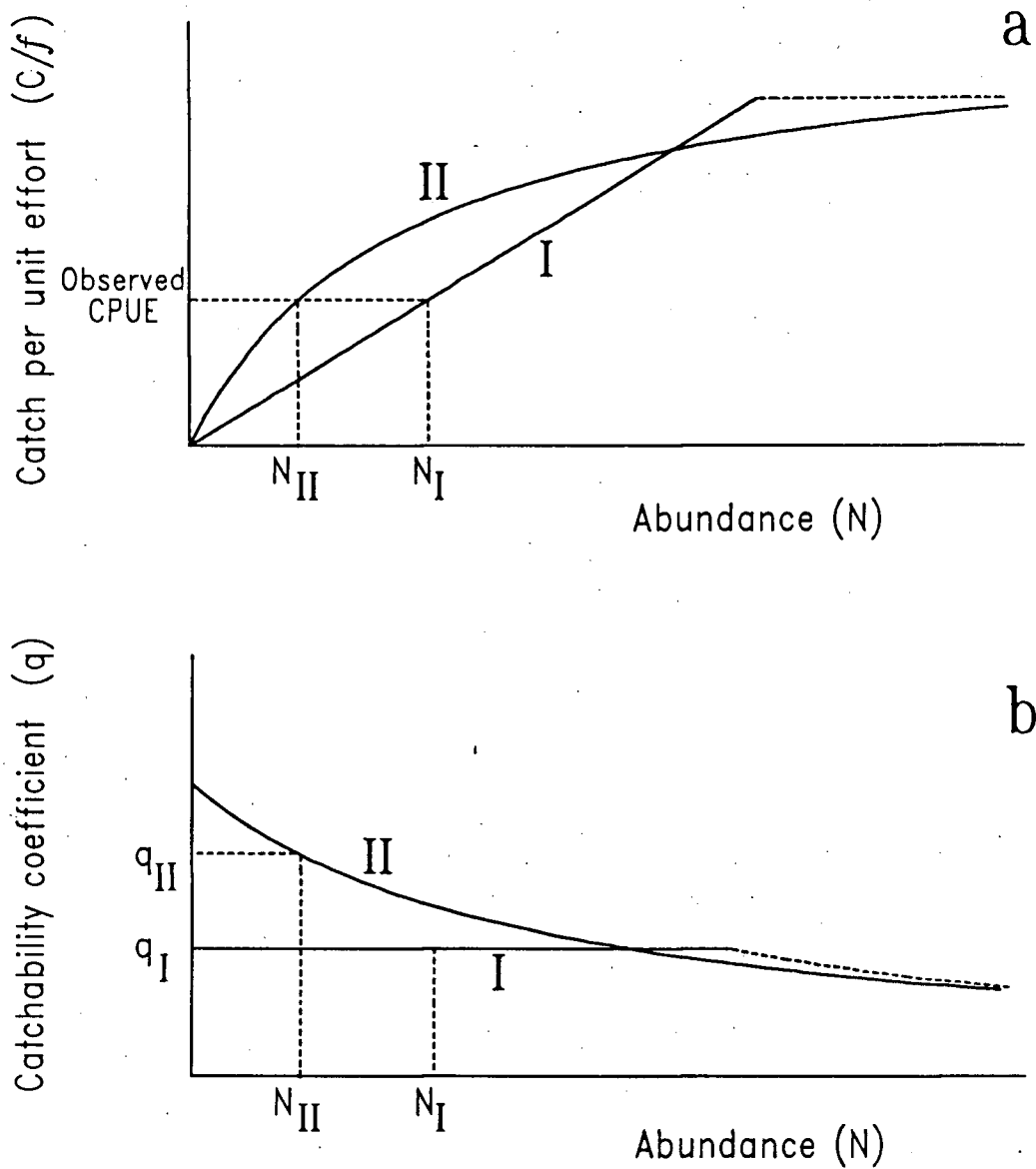


Figure 6.2. Comparison of two functional response forms for the fishery. Given the same observed CPUE, the type I response overestimates abundance (A) and underestimates the catchability coefficient (B) relative to the type II response.

and density within schools) as parameters rather than variables. A simpler model proposed by Fox (1974) has been widely applied in studies of functional responses in fisheries:

$$q = aN^{\beta} \quad (6.9)$$

where q is the catchability coefficient, N is the abundance of fish and a , and β are parameters to be estimated.

The relationship of Fox's (1974) model to functional response models is evident if the right hand side of equation 6.9 is substituted for q in equation 6.1 and the resulting expression is solved for C/f yielding

$$C/f = aN^{\beta+1} \quad (6.10)$$

Equation 6.10 was derived independently by MacCall (1976) and Ulltang (1976). Thus, while Fox's (1974) model is for density dependent catchability, it applies also to functional responses because when $\beta = 0$, q is constant and a type I response is indicated, for $-1 < \beta < 0$, q is inversely proportional to N and a type II response results and for $\beta > 0$, q is an increasing function of N and C/f versus N mimics the accelerating portion of a type III response. Thus, finding that $-1 < \beta < 0$ in equation 6.9 is the same as detecting a type II response (assuming f measures the total time (T) prey are exposed to the predator; e.g. Fig. 6.2).

Estimates of a and β are obtained by regression using log-transformed versions of equations 6.9 and 6.10. Thus, for equation 6.9 the regression equation is

$$\ln(q) = \ln(a) + \beta \ln(N) \quad (6.11)$$

Similarly, for equation 6.10 the regression equation is

$$\ln(C/f) = \ln(a) + (\beta+1)\ln(N) \quad (6.12)$$

Many of the studies I review below as evidence for type II functional responses in fisheries used equations 6.9-6.12 to test for density dependent catchability.

Evidence for Type II Responses

Based on Paloheimo and Dickie's model, the most likely situation to expect a type II response is in a fishery for schooling fish, where a large proportion of the fishing effort is spent searching for schools. Thus, it is not surprising that some of the first empirical tests of a type II response came from fisheries for various clupeoids (e.g. herring, anchovy) that show strong schooling behavior. Not coincidentally, these initial tests were made when several clupeoid stocks around the world were either near collapse or had already collapsed. For the theoretical mechanisms that may cause stock collapse in clupeoids see Clark (1974) and Ulltang (1980) and for a review of clupeoid stocks and their management see Murphy (1977) and various papers in Saville (1980).

Fox (1974) did not apply equation 6.9 by itself, but he incorporated the equation into a surplus production model that he fit to two species. He found $\beta = -0.3$ for Pacific sardine (*Sardinops sagax caerulea*) and $\beta = 0.4$ for Pacific yellowfin tuna (*Thunnus albacores*). Before Fox proposed his model, Schaaf and Huntsman (1972) had suggested that the catchability coefficient was inversely related to abundance in Atlantic menhaden (*Brevoortia tyrannus*). Later, Schaaf (1975) provided quantitative evidence when he fit Fox's model and found $\beta = -0.74$.

MacCall (1976) fit equation 6.11 to cohort analysis estimates (method of Tomlinson 1970) of catchability and abundance of Pacific sardine, and he found $\beta = -0.61$. Ulltang (1976) also used equation 6.11 to estimate the extent of density dependent catchability in the Norwegian herring (*Clupea harengus*) and he found $\beta = -1.376$. However, Ulltang (1976) thought the value of $\beta = -1.375$ was probably an overestimate because when $\beta < -1$, CPUE decreases with increasing abundance. These studies led Radovich (1976,1979) to question the use of CPUE as an index of abundance in fisheries for pelagic schooling fishes. Pope (1980) compared the fit of a density dependent catchability model (i.e. a type II response) with a density independent model using data from several North Sea herring fisheries, and he found that the density dependent model was more probable and fit most data sets better. The collapse of the world's largest fishery (i.e. Peruvian anchoveta; *Engraulis ringens*) may also be partly attributed to density dependent catchability (e.g. Murphy 1972; Paulik 1971; Csirke 1980; Beverton 1983).

More recently, Winters and Wheeler (1985) found that the catchability coefficient was inversely related to stock area for a number of northwest Atlantic herring populations. The primary mechanism was that fishing effort was able to operate more efficiently as the area occupied by the stock declined. The relationship held across stocks that occupied different sized areas and within stocks when stock area declined with abundance. The apparent decrease in stock area with declines in abundance found by Winters and Wheeler casts doubt on the type I response assumptions of the catch equation because most applications assume that stock area is constant (i.e. equation 6.1 is used instead of equation 6.3).

Not all studies of density dependent catchability have involved clupeids. Some studies have involved trawl fisheries for various groundfish. For example, Pope and Garrod (1975) and Garrod (1977) found that the catchability coefficient in two separate trawl fisheries for Arcto-Norwegian cod (*Gadus morhua*) was inversely related to stock biomass, although neither study provided estimates of β . Garrod (1977) also found that average catchability for three stocks of north Atlantic cod was inversely related to stock area. Houghton and Flatman (1981) found $\beta = -0.522$ when they fit equation 6.11 to catchability and biomass estimates from another northeast Atlantic cod stock that was exploited by a trawl fishery in the west-central North Sea. The relationship was not statistically significant when numbers were used instead of biomass. Archibald et al. (1983) hypothesized that catchability of Pacific ocean perch (*Sebastes alutus*) increased with decreasing abundance because the time spent searching increased with decreasing abundance and these changes in search time were not accounted for by the effort measure (i.e. hours trawled).

Angelsen and Olsen (1987) considered that catchability would be expected to vary with effort and density in their study of the Lofoten cod fishery. The effect of effort was expected because the fishery consisted of various stationary gear types (e.g. hand lines, long lines, gill nets and Danish seines) that became very dense during the height of the season and thus CPUE decreased due to interference and saturation effects (e.g. Rothschild 1977). Therefore, Angelsen and Olsen suggested a modification of the density dependent catchability model (eq. 6.9) as shown below.

$$q = aE^a N^\beta \quad (6.13)$$

or for equation 6.10

$$C = aE^{\alpha+1}N^{\beta+1} \quad (6.14)$$

In separate regressions on $\ln(q)$ on $\ln(E)$ and $\ln(q)$ on $\ln(N)$, they found that q was inversely related to effort and abundance for both longline and gillnet gear types (i.e. for longlines $\alpha = -1.967$, and $\beta = -0.852$ and for gillnets $\alpha = -1.660$, and $\beta = -0.826$). They combined the coefficients from the separate regressions by substituting the equations for q vs. E and q vs. N into the equation $q^2 = (C/EN)^2$ and solving for C . The resulting catch equations were

$$C_L = 9.697 \times 10^3 N^{0.574} E^{0.0165} \quad (6.15)$$

$$C_G = 2.969 \times 10^3 N^{0.587} E^{0.170} \quad (6.16)$$

where C_L and C_G are the catches by longlines and gillnets.

Angelsen and Olsen's (1987) study was unique because abundance estimates came from acoustic surveys. In addition, the surveys were detailed enough in one year to provide an estimate of within-year changes in availability. Thus, the equations above are the first estimates of density dependent and effort dependent catchability on an intra-annual time scale. The study does have a few problems, however.

The first problem is that Angelsen and Olsen (1987) applied the relative availability curve estimated in one year to total abundance estimates from 10 years, and then used the resulting within-year abundance estimates for all years in one regression. Thus, the X variate values (intra-annual abundances) for different years are not independent and would constitute pseudoreplicates (Hurlbert 1984). Therefore, the only data appropriate to include in statistical tests of within year density or effort effects on catchability are the data for the year

that the relative availability surveys were conducted.

The second problem concerns Angelsen and Olsen's (1987) method of combining the constants for effort and abundance; it ignores potential interactions between the two effects. Since the effects of effort and abundance undoubtedly interact to affect catch and q , it would be better to estimate the constants simultaneously by fitting equation 6.13 or 6.14. However, in practice it may be very hard to estimate the relative amount that catchability is affected by effort and abundance since these two factors commonly covary because of numerical responses. Under such circumstances, the estimates of α and β would be confounded (i.e. highly negatively correlated). The result of this confounding would be that two hypotheses, one that assumes large effects of density (i.e. large β) and small effects of effort (i.e. small α) and the other that assumes large effects of effort (i.e. large α) and small density effects (i.e. small β) would be equally consistent with the data.

A few studies have examined density dependent catchability in fisheries for anadromous species. The advantage of these studies is that estimates of abundance are often from direct counts of adults that return to freshwater to spawn. These estimates may be more reliable than abundance estimates for marine fishes that are based on a variety of stock reconstruction models (e.g. Tomlinson 1970, Pope 1972; also see Shardlow et al. 1985 for a different opinion). For example, Peterman (1980) found that the catchability coefficient in various native Indian food fisheries was inversely related to the abundance of various Fraser river sockeye salmon (*Oncorhynchus nerka*) stocks. Peterman was the first to draw direct analogies between Holling's (1959b) functional responses and predation by fishermen. Thus, Peterman characterized native Indian food fishermen as type II predators. One drawback of Peterman's (1980) study was

that the effort measure he used, number of permits, does easily relate to the total time prey are exposed to the predator (T). Peterman and Steer (1981) extended Peterman's (1980) work when they examined the functional responses of sportfishermen to the abundance of chinook salmon (*Oncorhynchus tshawytscha*). The authors found that the catchability coefficient was inversely related to abundance and that a type II response was indicated (see also Shardlow et al. 1985). Peterman (1980) and Peterman and Steer (1981) fit both the Fox (1974) model (i.e. eqs. 6.9-6.12) and Holling's (1959b) disc equation to the salmon fishery data.

In another study involving an anadromous species, Crecco and Savoy (1985) examined density dependent catchability in a commercial drift gillnet fishery in the Connecticut river for American shad (*Alosa sapidissima*). Using Fox's (1974) model, they found $\beta = -0.743$ (eq. 6.9) and $\beta = -0.724$ (eq. 6.10). The authors suggested that the primary mechanisms for density dependent catchability were strong schooling behavior during upriver migration by the shad coupled with nonrandom search behavior by shad fishermen. Crecco and Savoy (1985) also drew analogies with Holling's (1965) work and they suggested that another possible cause of density dependent catchability was increased handling times (emptying and resetting the nets) at high shad abundance levels.

Two studies examined functional responses in invertebrate fisheries. Beinssen (1979) found that $r=1196$ and $h=5$ (equal to a and t_h in the disc equation; eq. 5.2) and thus he found that abalone divers were type II predators. Hilborn and Walters (1987) modeled an abalone fishery using a type II functional response and sequential movement of effort to the most desirable area first (i.e. the numerical response) and found that a saturating relationship between CPUE and abundance resulted from simulations.

Type II Mechanisms in Fisheries

Athough Fox's (1974) model has been useful in describing the relationship between catchability and abundance, it has not provided any clues as to the possible mechanisms that cause density dependent catchability. Thus, most studies have only speculated on the mechanisms based on more detailed theoretical studies (e.g. Paloheimo and Dickie 1964; Rothschild 1977). Four main mechanisms have been cited as potential causes of type II responses in fisheries.

1. Gear saturation or limits to searching capacity.
2. Decrease in searching time available because of an increase in the proportion of time spent handling as abundance increases.
3. The areas searched by a unit of nominal effort represents a larger proportion of the area occupied by a clumped population as abundance decreases, because the area of the stock decreases with decreasing abundance (because of schooling by the fish) and/or because of nonrandom search by fishermen.
4. Fishing effort is directed at a subset of the total stock (i.e. particular age or size classes) that represents a large proportion of the total numbers and/or biomass and the proportion of the population composed of this subset increases as abundance decreases.

Saturation is analogous to satiation in natural predators. Gulland (1955) and Rothschild (1977) have provided theoretical models of saturation. Mechanism 1 is a possible cause of a type II response in Angelsen and Oslen's (1987) study of an inshore cod fishery and was cited as a potential cause in Peterman's (1980) Indian food fishery study.

Mechanism 2 follows directly from Holling's (1959b) disc equation (i.e. e.q. 5.2). Density dependent searching time was considered as the primary type II mechanism by Beinssen (1979) and Archibald et al. (1983). Peterman (1980), Crecco and Savoy (1985) and Hilborn and Walters (1987), considered mechanism 2 as one of a few possible alternative causes of type II responses in their studies.

Mechanism 3 was first suggested by Paloheimo and Dickie (1964). Most studies of density dependent catchability in clupeoids have cited mechanism 3 as the likely cause (e.g. Fox 1974; MacCall 1976; Radovich 1976; Ulltang 1976; Pope 1980; Winters and Wheeler 1985). Mechanism 3 has also been suggested as a possible cause of density dependent catchability in cod fisheries by Pope and Garrod (1975), in a shad fishery by Crecco and Savoy (1985), and in abalone fisheries by Hilborn and Walters (1987). Crecco and Savoy (1985) demonstrated that when overall shad abundance was low, fishermen targetted on the peak periods of migration and on areas of high local abundance.

Mechanism 4 was suggested as a possible cause of density dependent catchability in a North Sea cod fishery by Houghton and Flatman (1981). The ability of fishermen to direct their effort at age classes with high biomass has also been found in North Sea fisheries for other species (e.g. Cook 1984; Cook and Armstrong 1985). The next section considers type III responses in fisheries.

Type III Responses

A few studies have attempted to detect a type III response in fisheries. Peterman (1980) fit Fujii et al.'s (1978) generalized equation (i.e. eq. 5.8b) to data for the Indian food fishery, but he did not find parameter values (i.e. $c >$

$d \times t_h$) that were consistent with a type III response. Peterman and Steer (1981) also rejected the type III response in their analysis of chinook salmon sport fisheries. However, their rejection of the type III response appears to have been based on a visual inspection of the data. The authors suggested that a type III response could occur in fisheries if fish density was low and the area occupied by the fish was very large relative to the searching ability of fishermen (i.e. conditions where learning might act to increase the rate of effective search), but these conditions did not apply to the sport fisheries they examined which were either confined to rivers or to a small inlet.

Despite the lack of empirical evidence for type III responses in fisheries, the mechanisms for type III responses in natural predators reviewed in chapter 5 can also be expected to apply to fishermen. The three principle mechanisms for type III responses listed in chapter 5 were:

1. The predator is stimulated to spend a greater proportion of time hunting and/or hunting efficiency increases through learning when prey abundance increases.
2. The prey occur in patches of different densities and the predators feed more often in the high density patches and/or a limited number of spatial prey refugia are available and prey in refugia are less vulnerable to attack.
3. Switching by the predator between less abundant and more abundant prey (by various mechanisms, see below).

Mechanism 1 is probably the least likely mechanism to apply to fishermen. Undoubtedly, fishing is a learning process and learning might result in an increase in the rate of effective search. However, the circumstances in which to expect learning in fisheries (i.e. newly developing fisheries) are also likely to

be associated with high stock levels (i.e. virgin biomasses) and under such conditions any increase in the rate of effective search caused by learning would be offset by increased handling times. Furthermore, cases which have examined fisheries that have depleted populations (e.g. the clupeoid examples above), have not detected a decrease in catchability at low stock levels that would be predicted by a type III response (Fig. 5.4).

Fishermen are known to direct their effort at areas of high density (e.g. Saville and Bailey 1980; Cook and Armstrong 1985) and even at high biomass age or size classes of a stock (e.g. Cook 1984). This by itself would counteract type III effects. However, exploited fish populations are likely to have several possible refuge areas where they could escape from predation (e.g. areas of untrawlable bottom, areas closed by regulations). Thus mechanism 2. is very likely to operate in fisheries in spite of effort direction at concentrations.

Many of the world's fisheries involve more than one species. Thus, of the three type III mechanisms, the switching mechanism is probably the most likely of the above three mechanisms to apply to fishermen. Larkin (1979) stated:

..."man as a predator has an arsenal of technology with which he can be an accomplished switcher, and with modern processing and marketing techniques it may well be possible to be even more flexible in the future".

Given the likely applicability of switching to fisheries it is worth exploring in more detail the switching hypothesis as it applies to fishermen.

In considering switching hypotheses for fisheries, it is helpful to recall how the null hypothesis for switching in natural predators follows directly from the

multispecies disc equation (MSDE; i.e. equations 5.12-5.14). Recall that the switching null hypothesis was $NA_1/NA_2 = a_1N_1/a_2N_2$ (i.e. eq. 5.14). However, it is commonly assumed that fishermen are profit motivated (e.g. Clark 1976), and if so, the switching hypothesis presented for natural predators should be modified to account for the economic values of the species involved. The MSDE can easily be modified to calculate the attack rate (catch rate) in dollars by multiplying the catch rate in numbers ($CR = C/f$) by the price per fish. Thus, for the two fish species case:

$$V_1 = \frac{a_1 p_1 N_1 T}{1 + a_1 t_{h1} N_1 + a_2 t_{h2} N_2} \quad (6.17a)$$

$$V_2 = \frac{a_2 p_2 N_2 T}{1 + a_1 t_{h1} N_1 + a_2 t_{h2} N_2} \quad (6.17b)$$

where V_1 and V_2 are the catch rate in dollars (i.e. $V_i = (CR_i p_i)$; and p_1, p_2 are the price per fish in dollars (i.e. average weight per fish (kg) \times price per kg)). Since a profit maximizing fishermen is interested in the values V_1 and V_2 , the switching null hypothesis (i.e. no switching) for the fishery implies:

$$\frac{V_1}{V_2} = \frac{a_1 p_1}{a_2 p_2} \frac{N_1}{N_2} \quad (6.18)$$

Thus, given $a_1 = a_2$, equation 6.18 hypothesizes that in the absence of switching, the ratio of the catch rates in dollars of two species is proportional to their relative values and to their ratio of their numbers available in the environment (Fig 6.3a). A mixed species fishery which is completely nonselective with respect to species and without discards might fit this simple null model.

However, if fishermen are profit motivated, and if there is a physical way to select which species to catch, it would be better to catch the higher priced species in disproportionately larger quantities relative to the lower price species (i.e. fishermen should switch). if there is a physical way to select which Thus, I would expect a switching fishermen to increase his attack rate for the higher valued species. For example, switching for the case of the fishery could be incorporated into the MSDE in a way analogous to Murdoch and Oaten's derivation for natural predators (i.e. eqs. 5.15 & 5.16), except I will assume that rate of effective search for each species increases linearly with the proportion of the *value* of the species available (i.e. $p_i N_i$). Thus, I let $a_i = \lambda_i P_i$ where $P_i = p_i N_i / (p_1 N_1 + p_1 N_2)$ and with these substitutions, the functional response model for switching in the two prey case is

$$CR_i = \frac{\lambda_i P_i N_i T}{1 + \lambda_1 t_{h1} P_1 N_1 + \lambda_2 t_{h2} P_2 N_2} \quad (6.19)$$

Equation 6.15 results in a switching hypothesis of

$$\frac{CR_1}{CR_2} = \frac{\lambda_1}{\lambda_2} \frac{p_1^2 N_1^2}{p_2^2 N_2^2} \quad (6.20)$$

Note that in the case of the fishery, the catch rate depends on both abundance and price of each species. Thus, a switching fishermen is expected to increase the relative catch rate (i.e. CR_i also V_i) of the more valuable and/or more abundant species faster than linearly with changes in its relative abundance (Fig. 6.3 A). The switching curves are sigmoid and the null model is a straight line if plots are drawn in terms of the relative proportions caught and available (Fig. 6.3 B).

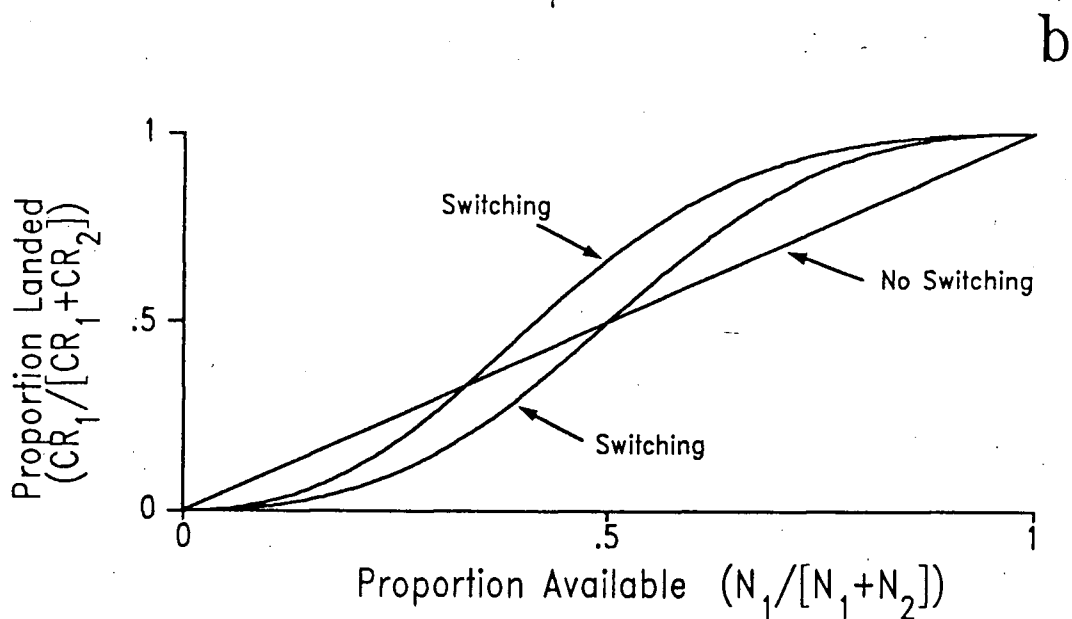
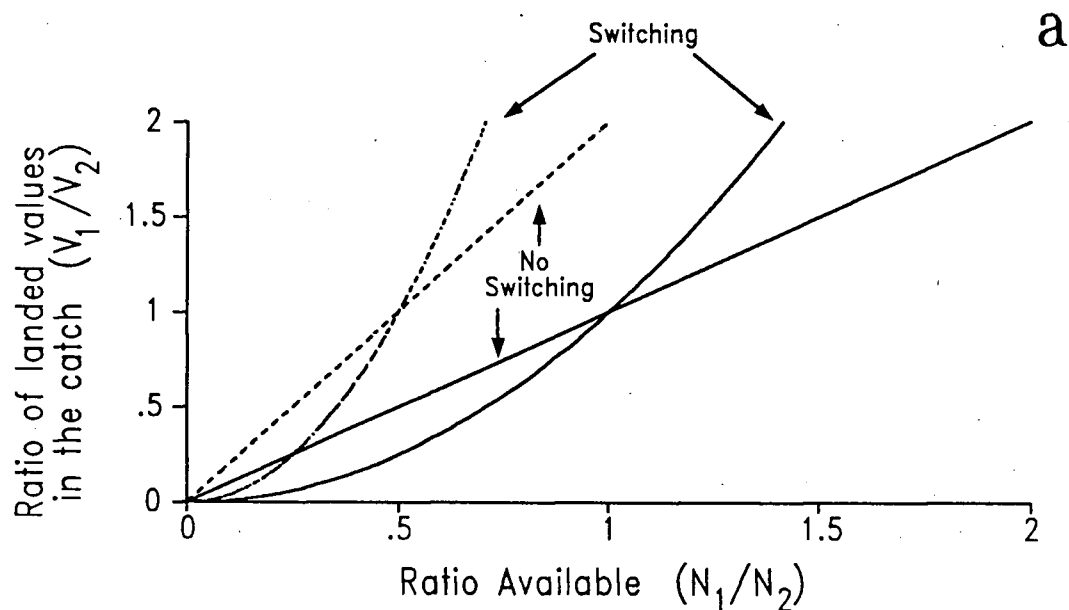


Figure 6.3. A. Implications of switching hypothesis for the fishery. Straight lines are for the ratios of catch rates in dollars for the case when $p_1 = p_2$ (solid line) and when $p_1 = 2p_2$ (dashed line). Curves are for switching. **B.** Switching hypothesis in fishery when catch rates and numbers available are expressed as proportions. Straight line denotes no switching, upper curve is for switching when $p_1 = 2p_2$, and lower curve is for switching when $p_1 = p_2$.

There are two primary mechanisms available for switching by fishermen. In cases where nonselective gear is used and species distributions overlap, fishermen may simply discard less valuable or otherwise undesirable species (i.e. switching mechanism 3 for natural predators; chapter 5). Alternatively, fishermen may attempt to target on particular species by fishing with selective gear or by spending a greater proportion of their time searching areas where more valuable species are concentrated (i.e. switching mechanism 1 for natural predators; chapter 5). The other two mechanisms for switching in natural predators (rate of detection dependent on recent experience, rate of successful attacks dependent on recent experience) could also apply to the fishery. For example, trawlers commonly use echo sounders to detect the presence of fish on or near the bottom. Some trawl captains claim they can tell the type of fish from a echo soundings and this ability would clearly depend on experience. The rate of successful attacks might also depend on recent experience because skippers must learn how to use the gear most effectively in the particular areas where different species are distributed (e.g. trawling on soft vs. hard bottom, flat vs. sloped bottom, etc.), and under various tidal conditions. However, these latter two mechanisms are probably much less common causes of switching in the fishery than the two primary mechanisms.

From examining equation 6.17, and considering the many variables that might affect fishermen's decisions, it is obvious that the form of the switching curve for any particular case will be affected by many factors. There is a void of research in this area, but one approach which seems promising is the application of optimal foraging theory (e.g. Stephens and Krebs 1986). The "prey" and "patch" models described by Stephens and Krebs (1986) are applicable to the discarding and targeting mechanisms above and could be used to determine

switching rules (i.e. what proportion of each species to take, and when to switch fishing grounds), and switching curves resulting from optimal foraging strategies (D. Gillis, Biological Sciences, Simon Fraser University, Burnaby, B.C. pers. comm.). However, in order to provide meaningful results however, these studies should modify the simple models to take account of fishing costs, risk, and state dependent foraging (e.g. the decision to discard may depend how much space is available in the vessel hold).

Finally, it is worth considering what factors peculiar to fisheries may affect the likelihood of detecting type III responses in existing data sets. In "single" species fisheries, the likely mechanisms for switching are learning, spatial refugia and other factors that cause an increase in the rate of effective search as fish density increases from low to moderate levels, or vice versa. The learning mechanism seems unlikely to apply to fisheries for the reasons mentioned above. Also, it does not appear that the rate of effective search declines in clupeoid fisheries when the population drops to low levels (several studies reviewed above found type II responses). In fact, the rate of effective search appears to increase even when the stocks have been depleted to very low levels. As these fisheries develop, the increases in fishing power due to improved gear technology and searching ability combined with the strong schooling behavior of the fish more than compensate for the decrease in the rate of effective search expected from decreased abundance. Clupeoid fishermen may simply act like type II predators.

However, type II responses also appear to describe fisheries data from nonclupeoid fisheries (e.g. Garrod 1977). Garrod's (1977) Arcto-Norwegian cod stock is actually part of a multispecies fishery where type III functional responses are more likely. Management may have kept abundance levels above

those where the rate of effective search declines. Alternatively, in fisheries where fishermen select target species by choosing particular gear types or areas, fishermen may simply switch to a different target species when their rate of effective search declines. Thus, in contrast with data from laboratory experiments with natural predators, fisheries data sets may not contain the range of observations over which the accelerating part of the type III response is generated. In unselective fisheries, fishermen may continue to catch species at low abundance levels, but unknown quantities of discarding may confound any attempts to discern the form of the functional response. As Murdoch and Oaten (1975) pointed out, the occurrence of switching does not necessarily imply a type III response.

Type IV Responses

The three main mechanisms for type IV responses in natural predators were reviewed in chapter 5: predator confusion by prey, predator disturbance by prey and group defense in prey. It is unlikely that any of these mechanisms operate in fisheries. In fact, it is ironic that schooling behavior that may act to confuse natural fish predators increases the vulnerability of fish to predation by man (e.g. Clark 1974; Clark and Mangel 1979).

Paloheimo and Dickie (1964) found conditions where their model gave a response similar to a type IV response. Their model predicted a decrease in the rate of attack as school radius increased (NA ; their $C(t)/t$) if the overall density of fish was constant and density within schools decreased as school radius increased (their Fig. 1 mislabelled as Fig. 2 in the paper). However, in order for these conditions to generate a type IV response to overall density, the additional

condition of school radius increasing with overall density must also be present.

Type II responses combined with a positive numerical response and competition could also result in apparent type IV responses. The mechanism in this case is analogous to predator disturbance by prey, except predators would be disturbing each other (i.e. interference competition). Thus, it is important to recognize that with most fisheries data sets apparent functional responses include interactions among fishermen; they are not analogous to results from experiments with natural predators where individual predators are used and the effects of competition or facilitation are thus excluded.

There is another mechanism for type IV responses in fisheries: fishermen are not all alike, and the poorer ones may only fish when (or where) fish are unusually abundant or valuable. In this case, the average catch/fishermen can easily decline as abundance increases, though for any single fishermen the response is monotonic increasing. Thus, it is important to distinguish between individual behavior and performance versus average per capita behavior of the aggregate fisherman population (C. J. Walters, Resource Ecology, Univ. of British Columbia, pers. comm.).

Chapter 7: Estimates of Abundance

Introduction

Any examination of functional responses requires estimates of prey abundance and percent mortality per predator (i.e. the catchability coefficient). However, obtaining these estimates for marine fisheries is problematic because direct estimates of fish populations are rarely available. Therefore, fisheries scientists have developed a variety of indirect methods for estimating demographic statistics. In this chapter, I first describe two related techniques that are used to estimate abundances and catchabilities of exploited fish populations from data on the age compositions of catches over time. Each technique is described in terms of the underlying mathematical model, data requirements and key assumptions. I apply these methods to three fish species that are the principal components of a multispecies trawl fishery in Hecate Strait. Next, I examine the sensitivity of estimates obtained from each technique to alternative assumed input parameters (i.e. fishing and natural mortality rates), and finally I compare the estimates obtained from the two techniques. Estimates of abundances and catchabilities obtained from the techniques are used in Chapter 8 which examines the functional responses of trawlers in Hecate Strait.

The first technique, Virtual Population Analysis (VPA; Fry 1949)⁴ was developed by Jones(1964), Murphy(1965), and Gulland(1965,1983). The second technique, Catch-at-AGE ANalysis with auxiliary information (CAGEAN; Deriso et al. 1985), is one of a variety of techniques (cf. Doubleday 1976; Pope 1977; Paloheimo 1980; Fournier & Archibald 1982; Pope and Shepherd 1982) developed

⁴ Fry originally coined the term "Virtual population" but his method differs from the techniques commonly referred to as Virtual Population Analysis (e.g. Gulland 1965, 1983)

as alternatives to VPA. I will use CAGEAN to denote the Deriso et al.'s (1985) technique (see below) and **CAGEAN** to denote the computer package that uses the technique. The two techniques have similar data requirements (e.g. estimates of numbers landed-at-age), but differ in some of their assumptions and estimation procedures. CAGEAN has more favorable statistical properties, but because of its recent development has only been applied to a few species. VPA is a simpler procedure that has been applied to many species. I chose to apply both methods for two reasons: (1) to determine whether the two techniques would provide similar estimates, and (2) to compare the sensitivity of estimates obtained from the two methods to alternative input parameters. Before proceeding with further details on the methods, the next section reviews the study area and the fishery used to examine functional responses.

Study Area and Fishery Description

My analysis of functional responses focused on the multispecies trawl fishery in Hecate Strait (Fig. 7.1). Landings statistics collected by Department of Fisheries and Oceans are available from various stock assessment documents (e.g. Westrheim 1980; Stocker 1981; Tyler and McFarlane 1985; Tyler et al. 1986). In addition to these basic statistics, the fishery has also been the subject of recent detailed analyses including a method for allotting effort among species (Westrheim 1983), estimation of relative fishing power of trawlers (Westrheim and Foucher 1985a), and various analyses of age composition data sampled from the landings (Ketchen 1961,1964,1970; Kennedy 1970; Chilton and Beamish 1982; Foucher and Fournier 1982; Foucher et al. 1984). In addition to these studies, Hecate Strait has been the focus of a five-year project that began in 1984 and that has the primary goal of developing an ecological basis for mixed-species

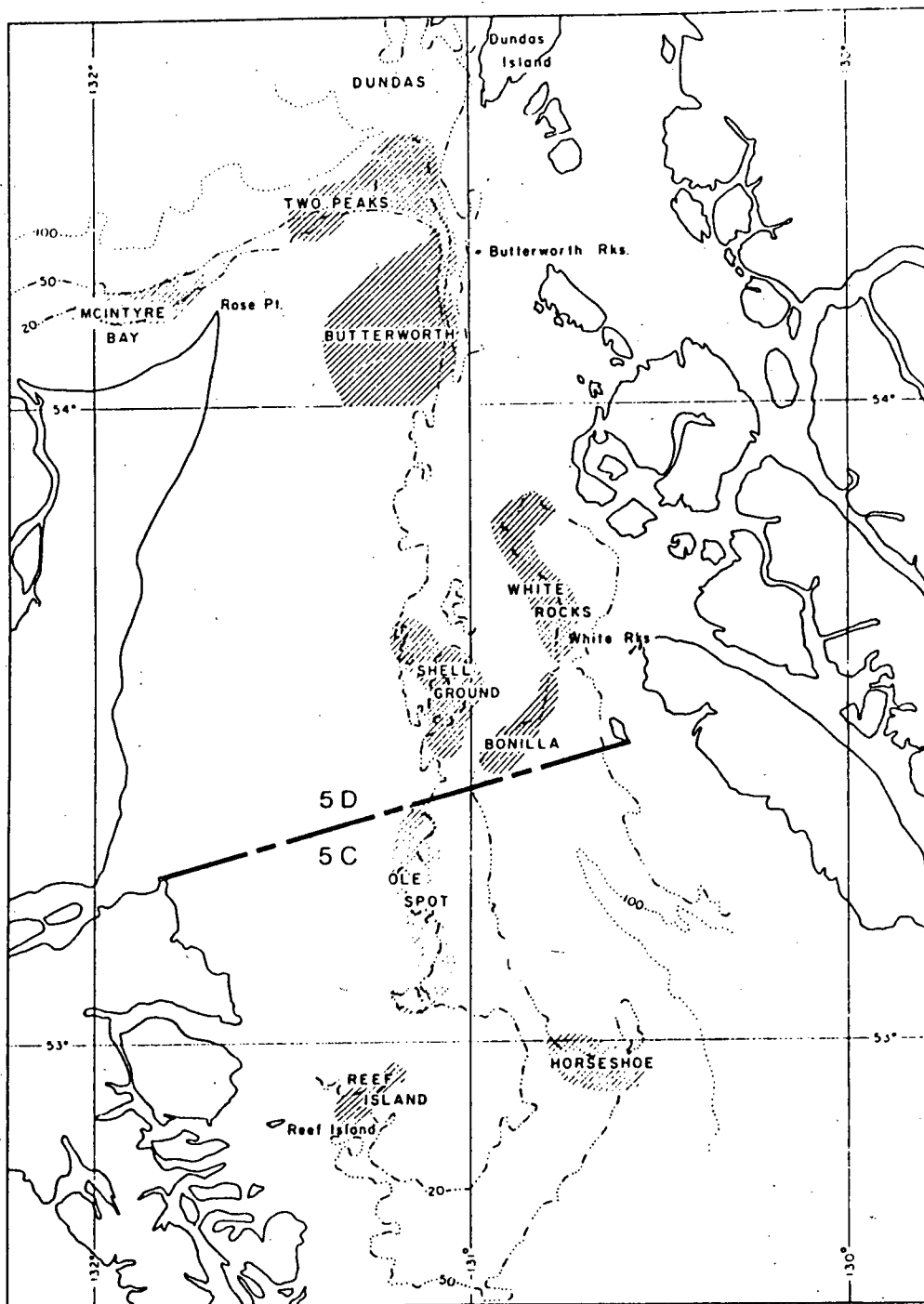


Figure 7.1. Map of principal fishing grounds and major statistical areas in Hecate Strait (from Westrheim 1983).

fisheries management (Tyler 1986, 1989). Using the wealth of information on this fishery available in the above studies, the description below briefly highlights the principal species involved, and general spatial and temporal patterns in their landings.

The principal species caught by the bottom trawl fishery in Hecate Strait are Pacific cod (*Gadus macrocephalus*), rock sole (*Lepidopsetta bilineata*) and English sole (*Parophrys vetulus*) (Westrheim and Foucher 1985b). Annual landings of these species have fluctuated cyclicly (Fig. 7.2). For statistical purposes, Hecate Strait has been divided into two major areas, 5C and 5D, each of which contains a few trawling grounds (Fig. 7.1). Detailed catch information including fishing ground and depth of capture have been collected by port samplers since the 1940's, however uncorrectable encoding errors make data unreliable for the pre-1956 period (Westrheim and Foucher 1985a).

Pacific cod and rock sole are caught in both major areas, but the only substantial landings of English sole come from area 5D (Westrheim and Foucher 1985b; Fargo 1985). Area 5D produced 67% of the cumulative landings of cod for the period 1960-81 (Foucher and Westrheim 1984) and 62% of the cumulative landings of rock sole for the period 1956-85 (Fargo 1986). The landings of both rock sole and English sole comprise primarily (>70%) females that are larger and more vulnerable than males (Fargo 1985).

Landings for all three species fluctuated seasonally and among grounds. Area 5C landings of cod and rock sole are from Horseshoe and Ole Spot grounds during April-September (cod) and June-October (rock sole), and from Reef Island-Cumshewa ground during January-June (cod) and April-May (rock sole; Fig. 7.1). In area 5D, the principal ground for all three species is Two

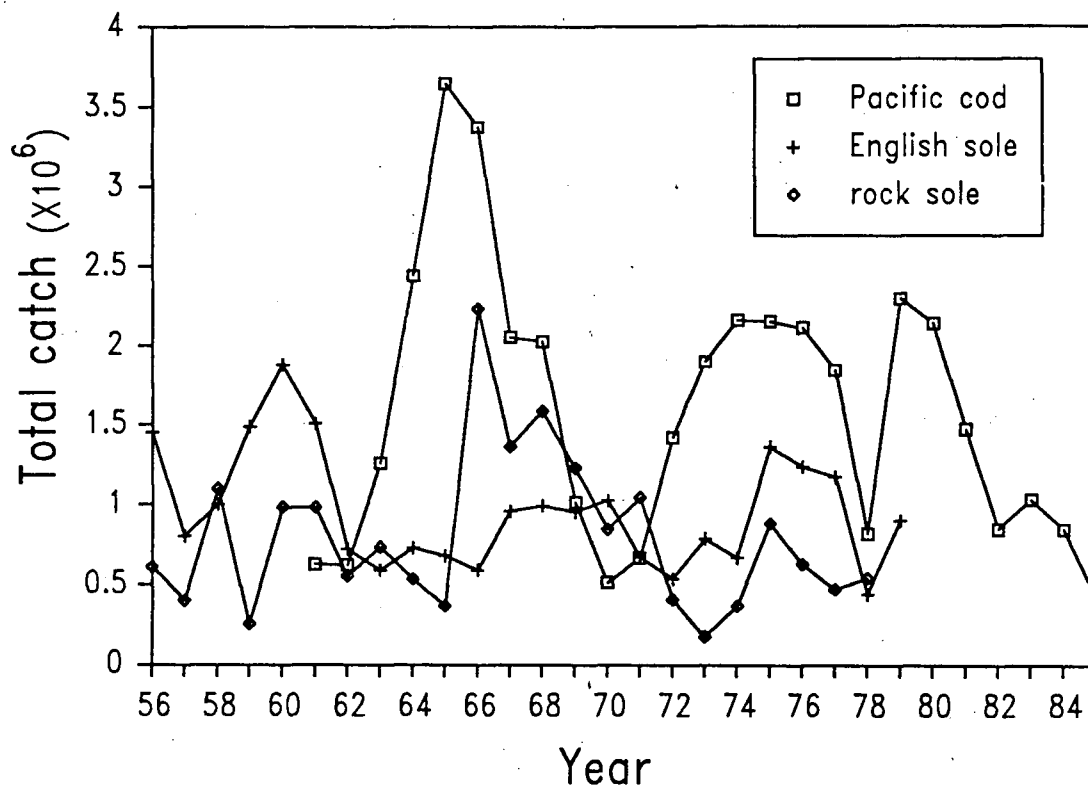


Figure 7.2. Estimated total numbers landed of Pacific cod (areas 5C+5D; ages 2-10; 1961-1985), English sole (area 5D; ages 3-17; 1956-1979) and rock sole (area 5D; ages 4-15; 1956-1978).

Peaks-Butterworth during April-September. A small amount of rock sole is also landed from Shell ground during these months (Fig. 7.1). During October-March, cod and English sole are landed from White Rock-Bonilla ground (Fig. 7.1; Westrheim and Foucher 1985b; Fargo 1985).

Principal depths of capture vary among species, seasons and years (Westrheim and Foucher 1985a). For example, the principal depths of capture of cod and English sole were 30-49 fathoms on Two Peak Butterworth ground, except for a few years when cod were caught at 10-19 fathoms. Rock sole have generally been caught in shallower water (10-19) fathoms, but have also had

substantial landings at 30-59 fathoms.

Data Preparation and Background Methods

Aging Methods

Both stock assessment methods used require estimates of the numbers of fish landed-at-age for each of the three species. Therefore, a brief description of the aging techniques used by the scientists at Pacific Biological Station for these three species is warranted.

Age composition samples for the three species were collected from commercial landings by port samplers stationed in Vancouver and Prince Rupert. Representative fishing grounds for age compositions were selected for each species based on the relative quantity of the landings from each ground and other criteria. Cod were aged from length frequencies (see below) and the representative grounds varied quarterly. White Rocks-Bonilla ground was used for quarters I (Jan.-March) and IV (Oct.-Dec.) and Horseshoe and Two Peaks-Butterworth grounds were used for quarters II and III (April-Sept.; Fig. 7.1; J. Westrheim pers. comm., Pacific Biological Station, Nanaimo, B.C.). Sample sizes taken for length frequencies ranged from 100-300 fish per month during the appropriate quarter(s) for each representative ground (Foucher and Westrheim 1984).

English and rock sole are aged from otoliths and Two Peaks-Butterworth ground was selected as the representative ground for both species (Fig. 7.1; Fargo 1985). Annual sample sizes have averaged 611 (range 100-957; no samples for 1972) for English sole and 596 (range 127-1345; no samples for 1965 and 1972) for rock sole (sample sizes are for females only for both

species; see below).

Of the three species, Pacific cod has been the most difficult to age reliably. Length frequencies and data from tagging experiments were used initially by Ketchen (1961,1964) who later showed that otoliths were of little use (Ketchen 1970). Concurrently, a technique using scales was described by Kennedy (1970), but in 1978 the use of the scale method was suspended pending validation because it was suspected of being inaccurate especially for older fish (Chilton & Beamish 1982). A method using dorsal fin rays yielded ages that were similar to those obtained from scales for younger fish, however it was thought that ages from fin rays were more reliable for older fish (Chilton & Beamish 1982). This method encountered technical problems however, that made it difficult to get consistently readable fin rays from port samples. At present the only technique being applied uses length frequencies following the general approach of Schnute & Fournier (1980) adapted for cod as described by Foucher & Fournier (1982) (in particular, see the appendix of their paper for details of the changes).

Any approach that uses length frequencies must deal with the problem of overlapping distributions (i.e. ranges of the length frequency distribution that likely contain fast growers from one age class mixed with slow growers of the next oldest age class). Early methods such as Harding (1949) and Cassie (1954) relied on graphical methods of separating out this overlap and assigning proportions to each group. For example, Cassie's (1954) method involves the visual inspection of a plot of cumulative frequencies versus length to identify inflection points. The choice of inflection point could then be evaluated using a χ^2 test. Schnute & Fournier's (1980) method is not completely objective. It identifies shapes of length frequency distributions that are consistent with simple biological

assumptions about growth (i.e. a von Bertalanffy growth curve).

Foucher and Fournier (1982) compared the estimated ages obtained from their method (termed the computer method) to those obtained from scales, Cassie's (1954) graphical method, and Ketchen's (1964) tagging experiment. Ages obtained from the graphical and computer method were similar to each other, but different from ages estimated by the scale method. Foucher and Fournier (1982) suggested that these differences were possibly due to errors in scale reading. They reached this conclusion based on an examination of mean lengths-at-age determined by the two methods. Estimates of mean lengths-at-age from the computer method were similar to those determined from tag returns (cf. Foucher et al. 1984).

In conclusion, Foucher and Fournier (1982) state that Pacific cod is a fast-growing species with a relatively small number of fished age classes, and therefore it should be an excellent candidate for aging by length frequency analysis. These characteristics of cod should minimize problems introduced by the lumping of older age classes common to length frequency techniques (Schnute & Fournier 1980). Proportions-at-age estimated using this techniques were used in my analysis.

In contrast to the problems encountered with cod, flatfish aging has proceeded rather smoothly. Both English sole and rock sole are aged using otoliths. Initially, ages were obtained from surface readings, but techniques using broken and burnt otoliths or thin cross sections were considered to be more accurate for older individuals, particularly for English sole. Preliminary results from age validation experiments using rock sole also suggest that readings from sectioned are more accurate (Fargo and Chilton (1987). Chilton and Beamish

(1982) describe the aging techniques in more detail.

All the ages for rock sole in my study were obtained from surface readings. The times series of ages for English sole is a mixture of surface and broken and burnt readings. In one experiment, approximately 600 English sole otoliths were aged by both techniques, so that the whole time series could be standardized to one method. I chose to follow the approach of J. Fargo (pers. comm., Pacific Biological Station, Nanaimo, B.C.) and convert all ages to surface ages because these ages make up 20 of the 26 years in the time series, and to maintain consistency between rock sole and English sole aging methods.

Estimating Numbers Landed-at-Age

I obtained tables of the number of fish landed-at-age for subsamples from the representative grounds for each species (flatfish, J. Fargo, cod, R. Foucher pers. comm. Pacific Biological Station, Nanaimo, B.C.). Given these estimates of numbers of fish landed-at-age in samples from the commercial fishery, the next step was to estimate the total numbers landed-at-age in the appropriate statistical areas. The statistical areas vary for the three species due to differences in stock delineation.

In the case of cod, the statistical areas are 5C+5D (Fig. 7.2) since tagging studies show that movement precludes stock separation within Hecate Strait (Westrheim 1984). The fishery for rock sole in Hecate Strait is considered to be made up of two stocks, one in area 5D the other in area 5C. This judgement is based on abundance trends in landing statistics, length frequency anomalies (Fargo 1985) and preliminary results from a tagging experiment

(Harling et al. 1982; Ketchen 1982). Age composition data are only available for the northern stock (i.e. area 5D). Hecate Strait is presumed to contain a single stock of English sole (i.e. in area 5D), based on landing statistics (Fargo 1985) and tagging experiments (Ketchen 1953).

In addition to divisions by stock, aging of the two flatfish species is also broken down by sex. Approximately 75% of the fishery for English sole involves females from 4-10 years of age (Fargo 1985). Similarly, approximately 80% of the landed weight of rock sole is comprised of females. Males are generally smaller, and therefore less vulnerable to the gear. Thus, only female English sole and rock sole were considered in the analysis. The exclusion of males is consistent with published stock assessments (Stocker 1981, Fargo 1985).

In summary, numbers landed-at-age in samples were inflated to total numbers landed in area 5C & 5D for cod and in area 5D for both rock sole and English sole females. The formula used was

$$N_i = (W/w) \times n \times p_i \quad (7.1)$$

where N is the total landings-at-age i , W is the total weight of landings, w is the weight of fish sampled, n is the number of fish sampled, p is the proportion of fish sampled in age group i .

For cod, equation 7.1 was applied to landings on a quarterly basis for each representative ground. For both flatfish species, equation 7.1 was applied to samples from Two Peaks-Butterworth ground. For years when no sample were taken (1972 for English sole, and 1965 and 1972 for rock sole, I used the average p_i calculated from the total landings for all years with samples; i.e. the average estimated proportion landed-at-age). All age compositions were extrapolated

to total landings for a standard calendar year (i.e. Jan.-Dec.). This deviates from past assessments for cod that used a "cod year" (i.e. April-March; cf. Stocker 1981 and Westrheim and Foucher 1985b). I chose the calendar year as my time stratum because it allowed for comparison between assessments of all three species. The estimated numbers landed-at-age for the three species are presented in Appendix A (Tables A1-A3).

Effort Data

In addition to estimates of numbers landed-at-age, estimates of fishing effort were also needed. I used effort data published in Tyler and Saunders (1987). Since all three species are caught in the same general area, and often in the same trawl haul, it was important that the effort used represented the effort "directed" at the particular species of interest. This is a problem common to multispecies fisheries and the main concern is not to include effort associated with incidental catches of a species that could result in misleading interpretations of stock abundance indices based on LPUE. The effort data I used were allocated to individual species by a method known as the Option 2 Method (Westrheim 1983). The method allots effort to a species based on an examination of the landings for designated time (quarter year), area (fishing ground), and depth (10 fathom intervals) strata. For example, if the depth strata 10-20 fm and 40-50 fm contained the largest and second largest total catches of English sole in quarter 2 (April-June) at Two Peaks-Butterworth ground, then the Option 2 effort for English sole would be the total effort exerted at those depths (toward all species) during quarter 2 on Two Peaks-Butterworth ground. Effort data were also standardized to account for changes in fishing power by

Westrheim and Foucher (1985a). The effort data used for each species are presented in Appendix A (Table A4.).

Models, Data Requirements and Assumptions

Virtual Population Analysis

Model Description - VPA

The technique of VPA is based on following a group of fish of the same birth year (a cohort) through time. The concept is most easily explained using a simple population model. If a cohort of fish is subject to a short fishery followed by a period of natural survival, then the cohort numbers next year ($t+1$) are related to the cohort numbers this year (t) by the following balance equation.

$$N_{t+1} = (N_t - C_t)s \quad (7.2)$$

where N is the number of fish, C is the catch, and s is an annual natural survival rate (from Ricker 1975, p.198 with $s=e^{-M}$). Note that equation 7.2 can be solved for N_t yielding

$$N_t = (N_{t+1})/s + C_t \quad (7.3)$$

Given estimates of N_{t+1} , C_t , and s , equation 7.3 is used recursively working backwards through time to solve for the N 's in previous years. This is the fundamental basis for VPA.

In most of the published literature, this simple concept is hidden in more complicated formulas written with instantaneous rates. The equations below from

Gulland (1965 cited in Pope 1972, also see Gulland 1983) are the most widely used.

$$N_{t+1} = N_t e^{-F_t - M} \quad (7.4)$$

$$C_t = \frac{F_t}{F_t + M} N_t (1 - e^{-F_t - M}) \quad (7.5)$$

where N and C are the abundance and catch in numbers, e is the base of natural logarithms, and F and M are the instantaneous rates of fishing and natural mortality respectively. The subscript t can refer to either year or age within a cohort. Equation 7.5, referred to as the *Catch Equation*, was first derived by Baranov (1918; cf. eqs. 6.1-6.3).

Equations 7.4 and 7.5 are for the more general case when the fishery occurs for a longer period and it is necessary to account for competing fishing and natural mortality. The main reason for their complicated appearance has more to do with notation than generality, however. Note that $e^{-F_t - M}$ of equation 7.4 is the total annual survival rate (from both fishing and natural causes). Therefore, $(1 - e^{-F_t - M})$ of equation 7.5 is the total annual death rate, and the ratio, $F/(F+M)$, is the proportion of deaths due to fishing. Equation 7.4 then, states that the numbers next year are the numbers this year times the survival rate, while 7.5 states that the catch is equal to a proportion of the total deaths due to fishing.

A third equation used in VPA comes from solving 7.4 for N_t and substituting the result into 7.5. It is

$$\frac{N_{t+1}}{C_t} = \frac{(F_t + M)e^{-F_t - M}}{F_t(1 - e^{-F_t - M})} \quad (7.6)$$

Data Requirements - VPA

Three items are required to start the estimation.

1. N_A s, the population sizes of the oldest age at which the each cohort was fished.
2. C_{at} , an estimate of the catch of each age a for the cohort for a series of years (t)
3. M , the natural mortality rate

For the *complete cohorts* (i.e. cohorts that have reached the oldest fished age (A) by the last year (T) of the catch data, shown as solid ellipses connected by solid lines in Fig. 7.3), VPA uses the catches of the oldest age (A) in each year t (i.e. C_{At} s enclosed by the solid rectangle in Fig 7.3), along with M and the terminal F values (i.e. F_{At} s) in equation 7.5 to calculate the numbers of fish of the oldest age each year (i.e. N_{At} s; item 1 above). For *incomplete cohorts* (i.e. cohorts that have not reached the oldest age by the last year of the catch data shown as open ellipses connected by dashed lines in Fig. 7.3), VPA uses the catches of each age (a) in the last year T (i.e. C_{aT} s enclosed by the dashed rectangle in Fig. 7.3), along with M and the age specific F values (i.e. F_{aT} s) in equation 7.5 to calculate the numbers of fish of the each age in the last year (i.e. N_{aT} s). For both complete cohorts and incomplete cohorts, estimation proceeds back in time through each cohort (i.e. along the diagonal lines in the direction indicated by the arrows in Fig. 7.3) using first equation 7.6 to solve for F_{T-1} and then equation 7.4 to solve for N_{A-1} and so on.

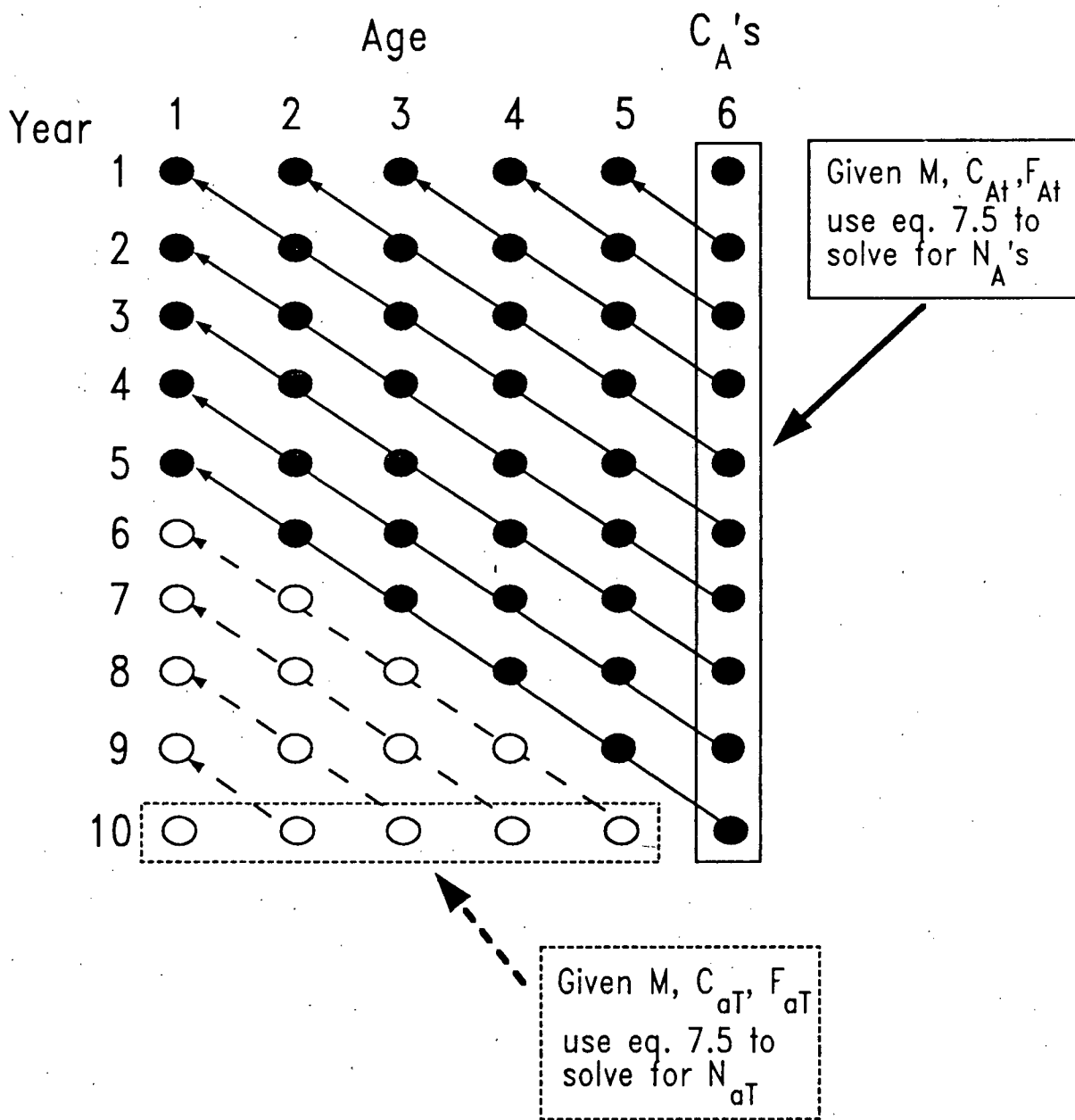


Figure 7.3. Schematic diagram of VPA method. Ellipses represent observations of catches-at-age for 10 years from a hypothetical fish population with 6 fished ages. Open ellipses connected by dashed diagonal lines denote incomplete cohorts and solid ellipses connected by solid diagonal lines denote complete cohorts. For further details see text. Figure 7.3 is modified from Figure 1 in Bradford and Peterman (1989).

F_{At} may be estimated from $F_{At} = qE_t$, where q is the average catchability coefficient for fully recruited ages, and E_t is the annual fishing effort. Numbers caught-at-age are commonly estimated by sampling and aging a portion of the landings as described above. The natural mortality rate, M , is either assumed at some arbitrary value or estimated along with the catchability coefficient by various regression methods (e.g. Gulland 1969; Paloheimo 1980). For incomplete cohorts, estimates of F_{aT} s are required for each age in the last year. Estimates of F_{aT} s are obtained from $F_{aT} = q_{aT}E_T$ where q_{aT} is the catchability coefficient for each age a in year T . Estimates of q_{aT} are obtained from the q_{at} s for each age averaged over complete cohorts after the initial pass of the VPA (see equation 7.14 below).

Model Assumptions - VPA

There are four principal assumptions of VPA (Walters 1987a).

1. N represents a closed group of fish. There is no immigration or emigration.
2. The odds of dying from either fishing or natural causes are the same at each moment during the year.⁵
3. M is constant over time and ages.
4. $F_{a,t}$ is known (i.e. $F_{a,t} = q_{a,t}E_t$) for all ages a in the last (most recent) year t , and for the oldest age in all other years.

Migration effects on VPA were investigated by Ulltang (1977). He developed a model to keep track of cohort numbers for the hypothetical case where a cohort continuously migrates from area A to area B at a constant rate. If emigration were included in the estimate of M for area A, VPA could be

⁵ Assumption 2 applies only to continuous fishery version (i.e. to equations 7.4-7.6, not equations 7.2 and 7.3).

used. However, he found no simple way to account for immigration to area B. In practice, the conditions of assumption 1 are approximated by choosing the area of the fishery large enough to minimize or balance additions and losses due to migration (e.g. the choice of areas 5C and 5D for Pacific cod).

Ulltang (1977) and Sims (1982) investigated the effects of violations of assumption 2 on N estimates from VPA. Ulltang concluded that an uneven distribution of M or F throughout the year produced negligible errors in VPA. Sims concluded that errors were not severe unless M was large and the fishery was seasonal with heavy exploitation at one end of the year or the other. Walters (1987a) stated that assumption 2 was not too critical; F & M estimates can be viewed as integrals across seasonally varying rates.

Violations of assumption 3 are difficult to detect due to confounding with possible changes in F with age and time. Effects of errors in M were investigated by Agger et al. (1973) and Ulltang (1977). They concluded that errors in M were transferred to estimates of N and F . If M was overestimated, then N was overestimated and vice versa, but relative N values from year to year were approximately correct. Overestimates of M result in underestimates of F and vice versa. Trends in true M with time were converted to trends in F estimates from VPA. Bradford and Peterman (1989) showed that incorrect values of M or F caused spurious time trends in N_t estimates obtained from incomplete cohorts. Bradford and Peterman (1989) found that the magnitude of the spurious time trend was inversely related to the ratio of F_T/M . These time trends disappeared however if the F_T values for these incomplete cohorts were calculated from the results of an initial VPA and the VPA was repeated iteratively until starting and ending F_T values converged (method of Rivard 1983). Lapointe et al. (1989) found that a time series of increasing fishing mortality rates coupled

with an incorrect value of M caused spurious time trends in abundance estimates for complete cohorts. The magnitude of the bias depends on the range of cumulative fishing mortality rates among cohorts that were present during the beginning and end of the increasing F period. Given the potential effects of an incorrect choice of M , or time trends in M , Walters (1987a) cautioned users of VPA to only consider relative rather than absolute results.

Assumption 4 was investigated by Pope (1972). He showed that incorrect choice of terminal F_T values introduced errors in N_T estimates particularly for the last few years of a catch-at-age data set, but these errors were small when cumulative fishing mortality over the life of the cohort is >2.0 . For a cohort that is fished for 10 years, this represents an average annual exploitation rate of $>18\%$. This property of VPA limits its utility in providing estimates of current abundances because the current estimates are the sums over the incomplete cohorts that have been fished for only a few years (i.e. low cumulative fishing mortality). Therefore, estimates for recent cohorts are generally most subject to error caused by incorrect terminal F_T values. Pope (1972) suggests that N_T estimates can be errant for all years if F is low compared to M . When terminal F_T are estimated from $F_T = qE_T$, it is important that effort be standardized such that q is constant over the time period used (e.g. Gulland 1956a). Effort standardization is particularly essential to the regression methods used to estimate M and q (e.g. Paloheimo 1980).

In addition to these assumptions, errors in aging catch samples, may introduce errors in VPA. Walters (1987a) noted that aging errors mask variations in numbers at a given age across years as fish will be incorrectly assigned from small to large cohorts and vice versa. There is no simple way to correct for aging errors. Walters suggested reallocating the age sample according to various

assumptions about the magnitude of errors. Other methods (cf. Fournier and Archibald 1982; Deriso et al. 1985) assume a particular distribution for the aging errors and adjust their calculations accordingly. The method of Deriso et al. (1985) also permits pooling of older ages, where aging errors are more likely to occur particularly when fish are aged from bone structures (e.g. otoliths) or other hard parts (e.g. scales, fin rays).

In conclusion, because violations of VPA may result in erroneous estimates of abundances and fishing mortalities, it is important to interpret the results carefully. Possible violations of assumptions 1,2,4 may be evaluated to some extent for individual data sets. Violations of the constant natural mortality assumption are difficult to detect, and dictate the use of only relative results. The effects of aging errors are not addressed by VPA alone, but may be evaluated through simulation given some assumed distribution for the errors. More recent techniques (e.g. Deriso et al. 1985) may be less sensitive to the effects of aging errors.

Catch-at-age Analysis with Auxiliary Information (CAGEAN)

Model Description - CAGEAN

The goal of CAGEAN (Deriso et al. 1985) and its predecessors is the same as that of VPA: estimation of cohort numbers and fishing mortalities. The primary impetus for CAGEAN came from the recognition that VPA estimates more parameters than there are observations. For example, a catch-at-age data set with 20 years and 10 ages would contain 200 observations. The VPA equations using these data contain 221 unknowns (i.e. 200 F values, M, and the N values for the oldest age in each year;

N_A s). In order for VPA equations to be solved, M and the N values (or F_T values) must be supplied. A second reason for the development of methods such as CAGEAN is that VPA does not provide very reliable estimates of current abundance due to dependence of the most recent estimates on the terminal F_T values. CAGEAN offers two remedies for these problems. The first is to reduce the number of parameters to be estimated from the catch-at-age data and the second is to use additional data (called *auxiliary information*) to help define uncertain parameters (e.g. F values) and to increase the number of observations. The resulting model has three components: a catch-at-age component using the catch equation (eq. 7.5), a component that relates fishing mortality to fishing effort, and a spawner-recruit component that relates the number of recruits (i.e. offspring surviving to first fished age) to the number of spawners (i.e. parents).

CAGEAN's first component is aimed at reducing the number of parameters to be estimated from the catch data. Like VPA and most other methods, CAGEAN starts with the catch equation (eq. 7.5), however the form of the catch equation used by CAGEAN comes from combining equations 7.4 and 7.5. Given these two equations, it follows that catch can be related to recruitment abundance (i.e. abundance at first fished age) by

$$C_{a,t} = \frac{F_{a,t}}{F_{a,t} + M} N_{r,t} (1 - e^{-F_{a,t} - M}) e^{\sum(-F_{a,t} - M)} \quad (7.7)$$

where all symbols are the same as in 7.5 except that $N_{r,t}$ is the recruitment abundance, and the subscripts a and t denote age and year. The term $e^{\sum(-F_{a,t} - M)}$ is the cumulative survival rate from time of first recruitment to time t . For clarity, the notation of equation 7.7 has been simplified from that of Deriso et al. (1985; eq. 7, p. 817).

Unfortunately, like VPA, this restatement of the catch equation still has more parameters than observations. The key step to reduce the number of parameters was suggested by Pope (MS 1974 cited in Doubleday, 1976). Pope's idea was that the fishing mortality rate F at a given age and year could be modeled as the product of a year effect F_t (due to changes in fishing effort), and an age selectivity effect S_a (due to gear selection or partial recruitment).

$$F_{a,t} = F_t \times S_a \quad (7.8)$$

This model reduces the number of fishing mortality parameters from $A \times T$ years to $A + T$ (A age selectivity effects, and T fishing mortalities). Equation 7.8 is commonly referred to as the *separability assumption*. CAGEAN assumes at least one of the $S_a = 1$ because the age effects can only be measured relative to the total fishing rate (F_t) for each year. The separability assumption makes estimation possible. The estimation is accomplished by nonlinear least squares, with the residual sums of squares (SSQ) given by

$$SSQ(\text{catch}) = \sum_{a,t} (\log C'_{a,t} - \log C_{a,t})^2 \quad (7.9)$$

where $C'_{a,t}$ is the predicted catch from equation 7.7, and $C_{a,t}$ is the observed catch. Like VPA, CAGEAN uses an assumed M that must be estimated outside the model. Equation 7.9, CAGEAN's first component, is nearly identical to that of Doubleday (1976). CAGEAN diverges from this earlier work in the use of auxiliary information.

CAGEAN uses two types of auxiliary information to help with parameter estimates. CAGEAN's second component uses fishing effort to provide more information about the

F_t estimates of equation 7.8. The model for the second component is

$$F_t = q \times E_t \times e^{v_1} \quad (7.10)$$

where F_t is the full-recruitment fishing mortality, E_t is the fishing effort, q is the catchability coefficient, and e^{v_1} represents lognormal random variability about the relationship. This form of fishing mortality-effort relationship was first used in the catch-at-age estimation scheme of Fournier & Archibald (1982). The sums of squares for the second component is

$$SSQ(\text{effort}) = \lambda_1 \sum_t (\log(F_t) - \log(qE_t))^2 \quad (7.11)$$

where λ_1 is the ratio of variances (variance of observed logarithm of catch from that predicted by 7.7 divided by the variance of observed logarithm of effort). This second component, called an auxiliary sums of squares, is added to the least squares equation 7.9. Deriso et al. (1985) consider λ_1 to be a weighting term used to adjust the amount of influence of the effort data. A very large value for λ_1 would result estimates of F_t that are exactly proportional to E_t .

The third component of CAGEAN was developed to help bound the $N_{r,t}$ estimates of equation 7.7. Again, following Fournier & Archibald (1982), Deriso et al. (1985) assume that recruitment is based on a Ricker (1954) spawner-recruit function with lognormal variability. The model is

$$N_{r,t+r} = S_t e^{a-bS_t+v_2} \quad (7.12)$$

where N is the recruitment abundance, S is the spawning stock egg production (different from S_a ; the age specific selection coefficient), a and b are stock-recruitment coefficients, v_2 is a random variable, and the subscripts r and t denote recruitment age and year. S_t is the sum over all ages of the $N_{a,t} \times e_a$, where e_a is the age specific net fecundity (i.e. percent mature \times fecundity). Estimates of age specific net fecundities for each species are presented in Appendix A (Table A5.). Note that the third component does not add any observations; $N_{r,t}$ is estimated simultaneously in equations 7.7 and 7.12 of the model. The sums of squares for the third component is

$$SSQ(\text{spawn}) = \lambda_2 \sum_t [\log(N_{r,t+r}) - (\log S_t + a - b S_t)]^2 \quad (7.13)$$

where λ_2 is the ratio of variances as in λ_1 except the denominator is the variance of the stock-recruitment relationship. A high value for λ_2 would result in recruitment abundance estimates that are a deterministic function of spawning stock. Equation 7.13 is added to equations 7.9 and 7.11 to yield the complete CAGEAN model, where the problem is to find the parameters that minimize $SSQ(\text{catch}) + SSQ(\text{effort}) + SSQ(\text{spawn})$.

When all three components are included (i.e. $\lambda_1, \lambda_2 > 0$), CAGEAN estimates the following parameters:

1. Full-recruit fishing mortality rates ($F_t s$; i.e. the fishing mortality rates on ages with $S_a s = 1$) for each year of catch data (a total of T values).
2. Age specific selection coefficients ($S_a s$) for each age as desired (a maximum of $A-1$ values).
3. The abundances for the youngest age class each year for all ages in the first year (a total of $T+A-1$ abundances).

4. A catchability coefficient (q).
5. Two stock-recruitment model parameters (a and b).

Thus, CAGEAN estimates a maximum of $2A+2T-1$ parameters from $A \times T+T$ observations.

Data Requirements - CAGEAN

The data requirements for CAGEAN are as follows:

1. Estimates of numbers caught-at-age
2. An estimate of natural mortality (M)
3. A time series of fishing effort
4. Estimates of net fecundities-at-age

To start the nonlinear estimation, CAGEAN requires starting guesses for each of the parameters (see above). However, if supplied with an estimate of the terminal fishing mortality rate in the last year, the CAGEAN program will generate its own starting values using a routine called COHORT (Deriso et al. 1985). The CAGEAN program is also designed to permit estimation of parameters using just the first component or any combination of the first component and the other two components. Therefore, estimates can be obtained with data for items 1 and 2 only. However, as noted by Deriso et al. (1985), the earlier work of Doubleday (1976) and Pope (1977) showed that catch-at-age data alone are insufficient to estimate abundance reliably because estimated fishing mortality and estimated abundance are negatively correlated.

Model Assumptions - CAGEAN

Deriso et al. (1985) list six assumptions for the model (see page 818).

1. Catch is given by Baranov catch equation times a lognormal random variable.
2. Natural mortality, M , is fixed at known value.
3. Fishing mortality is separable into an age-dependent factor (selectivity) and a year-dependent factor (full recruitment fishing mortality).
4. Full recruitment fishing mortality is proportional to fishing effort times a log-normal random variable.
5. Recruitment is given by a Ricker spawner-recruit function times a log-normal random variable.
6. The variance ratios, λ_1 and λ_2 are fixed at known values.

Assumptions 1 and 2 are shared with VPA. Implicit in assumption 1 are the closed population assumption and "equal odds of mortality" assumption of VPA. Although violations of these first two assumptions have not been investigated in CAGEAN, similar conclusions to those found for VPA could be expected. The procedure of Fournier & Archibald (1982) permits estimation of M , but the accuracy of the estimate is hard to evaluate with actual rather than simulated data.

The validity of the separability assumption rests on selectivity-at-age remaining constant over time. If there are known changes in selectivity due to changes in gear, then **CAGEAN** permits division of the data into separate selectivity estimation periods. Accounting for more subtle changes, for example,

due to changing market conditions, would be more difficult.

The last three assumptions concern the auxiliary data. The key to meeting assumption 4 is a standardized effort time series, such that F_t is proportional to effort. Note however, that CAGEAN permits variability about equation 7.10, with the amount of variability depending on the choice of λ_1 . As with selectivity, CAGEAN permits the division of the time series into "catchability periods" if changes have occurred that cannot be accounted for by standardization. CAGEAN also permits flexibility in choice of the stock recruitment function in assumption 5, but modifications to the computer program are required.

The effect of assumptions 4 and 5 on parameter estimates depends on the values assumed for the variance ratios, λ_1 and λ_2 . Large values (e.g. 1000) for the variance ratios mean that equations 7.10 and 7.12 hold exactly while small values (e.g. 0.0001) allow large variability to occur about the relationships and greater reliance on the catch data for parameter estimates. Deriso et al. (1985) examined the sensitivity of parameter estimates to λ values using data from Pacific halibut and VPA estimates for complete cohorts as a benchmark. They found errors in estimates were reduced when medium or large values were used when compared to errors from estimates using no auxiliary information. Since the choice of λ values is arbitrary, experimenting with different values is warranted.

Application of Models and Specific Methods

Computer Programs and Starting Input Parameters

Two computer programs were used for the estimation. VPA estimates were obtained from CATANAL (Walters 1987a) and the program CAGEAN

(version 2.0) was used in the *CAGEAN* estimates. Both programs were implemented on a IBM compatible microcomputer. *CATANAL* was obtained from C. Walters, Resource Ecology, Univ. British Columbia, Vancouver, B.C. V6T 1W5 and *CAGEAN* was obtained from P. Neal, International Pacific Halibut Commission, P.O. Box 95009, Seattle, WA 98145-2009.

Starting natural mortality (M) and catchability (q) values for VPA were estimated by *CATANAL* using the regression technique of Paloheimo (1980). Estimates were highly variable depending on the range of ages included in the regression. I selected M and q estimates that were consistent with published values (Westrheim and Foucher 1985, Fargo 1985, Walters et al. 1982) for lack of any independent reliable estimates. Terminal fishing mortalities (F_T s) for the initial runs of VPA were calculated by *CATANAL* from $F_T = qE_T$. Subsequent VPA iterations use average age specific q 's and effort to estimate terminal F values for incomplete cohorts with the same equation. I repeated iterations (2-4 times) until average age specific q 's estimated in successive runs converged (i.e. the iterative method of Rivard 1983). This eliminates the possibility of the spurious time trends discussed by Bradford & Peterman (1989). Estimates of M and terminal F used in VPA were also supplied to an initialization routine (i.e. COHORT) in *CAGEAN* that calculates starting parameter values for the nonlinear estimation. Initial parameter values for each species are shown in Appendix A (Tables A6-A7.).

Data for the same ages and years were used in both techniques, but older ages were pooled in *CAGEAN* to reduce possible affects of aging errors. The ages pooled were ages 8-10 for cod, ages 11-17 for English sole and ages 11-15 for rock sole. Age specific selection coefficients were estimated for ages 2,3 for cod, ages 3,4,5 and 11-17 (as a group; a total of 4

S_a s) for English sole and ages 4,5 and 11-15 (a total of 3 S_a s) for rock sole. For a table of the catch-at-age data and starting parameters for each species, see Appendix A (Tables A1-A7).

Estimates of Abundances and Catchabilities

Abundance estimates for VPA came directly from the VPA equations. For CAGEAN, abundance estimates for older ages were calculated from equation 7.4 using the estimates of recruitment abundances, fishing mortalities in each year, and the assumed M value. Full-recruit fishing mortalities were multiplied by the S_a values for all ages with $S_a < 1.0$.

Catchability coefficients for VPA were estimated for each year t using the equation

$$q_t = \frac{\Sigma C_t M}{E_t (\Sigma N_t - \Sigma N_{t+1} - \Sigma C_t)} \quad (7.14)$$

where ΣC_t , ΣN_t are the catches and abundances summed over fully recruited ages in year t (i.e. ages 4-10 for cod; 6-10 for English sole and rock sole), and ΣN_{t+1} is the abundance summed over the first fully recruited age + 1 to the last fully recruited age + 1 for each species in year $t+1$. Thus, VPA can only estimate catchabilities for $T-1$ years because ΣN_{t+1} is not available for the last year. I used fully recruited ages in the VPA calculations so that the catchability estimates could be compared with those obtained from CAGEAN (see below). CAGEAN's estimates one catchability coefficient that represents the relationship of F_t to E_t as determined by equations 7.10, 7.11. In order to estimate annual catchability coefficients, I rearranged equation 7.10 yielding

$$q_t = F_t/E_t = q \times e^{\epsilon_t} \quad (7.15)$$

Note that dividing F_t by E_t is equivalent to multiplying the average q estimated by CAGEAN by e^{ϵ_t} where ϵ_t are the residuals from equation 7.11.

Sensitivity Analyses

I estimated the sensitivity of each method to alternative starting parameter values by comparing estimates of abundances and catchability coefficients obtained from the "best" estimates of input parameters $\pm 50\%$ for each species. Thus, I compared VPA estimates obtained from M_B (subscript B denotes the best estimate) with estimates obtained from $M_B + 50\%$ and $M_B - 50\%$, and similarly for q_B and $q_B \pm 50\%$. I made the same comparisons for CAGEAN estimates obtained from M_B , $M_B + 50\%$, and $M_B - 50\%$ and F_B , $F_B + 50\%$, and $F_B - 50\%$. I used the alternative input parameters, M and F and the routine COHORT to generate different starting values for the nonlinear estimation. These starting values, along with M were then input into CAGEAN while holding λ_1 and λ_2 fixed at 0.5.

I also investigated the sensitivity of CAGEAN estimates to the choice of λ values. I compared estimates obtained from five alternative λ value combinations; (1) $\lambda_1, \lambda_2 = 0$, (2) $\lambda_1, \lambda_2 = 0.5$, (3) $\lambda_1, \lambda_2 = 100.0$, (4) $\lambda_1 = 0, \lambda_2 = 1.0$, and (5) $\lambda_1 = 1.0, \lambda_2 = 0$. I selected these five combinations because they represent the following five qualitative uses of the auxiliary data: (1) no auxiliary data, (2) a moderate amount of auxiliary data (combined weight same as catch data), (3) heavy reliance on the auxiliary data, (4) auxiliary spawner-recruit data only, and (5) auxiliary effort data only. In my comparisons of estimates obtained from different λ values, I used the

M_B and F_B estimates for each species.

Finally, I compared the estimates of abundances and catchabilities obtained from the CAGEAN and VPA. In this comparison, I used the best estimates of the input parameters and $\lambda_1, \lambda_2=0.5$ because the previous sensitivity analyses within methods gave estimates that were highly correlated and showed very similar temporal patterns.

Results

"Best" Estimates - VPA and CAGEAN

Estimates of abundance obtained from VPA and CAGEAN using the best estimates of input parameters are shown in figure 7.4. Estimates from the two methods are very similar and a more detailed comparison is presented below. All three species show cyclical fluctuations in estimated abundances over time (Fig. 7.4). Cod is the most abundant species with a peak abundance in 1964 and a trough in 1970. A second peak in cod abundance is evident in the mid to late 1970's although it is much less pronounced than the earlier peak (Fig 7.4). Based on pre-1960 LPUE data and the fact that cod abundance appears to have increased in recent years (Fargo and Tyler 1989), troughs in cod abundance have also occurred in the late 1950's and early-mid 1980's. Thus, for the 40-50 yrs for which there are data, cod abundance has fluctuated cyclically with a period of 9-11 yrs. The cause of the cyclical trends is unknown, but studies have found that cod recruitment rates are positively correlated with the abundance of herring in Hecate Strait (Walters et al. 1986) and with above average late winter water temperatures (Tyler and Westrheim 1986) and negatively correlated with northward water-mass transport (Tyler and Westrheim 1986).

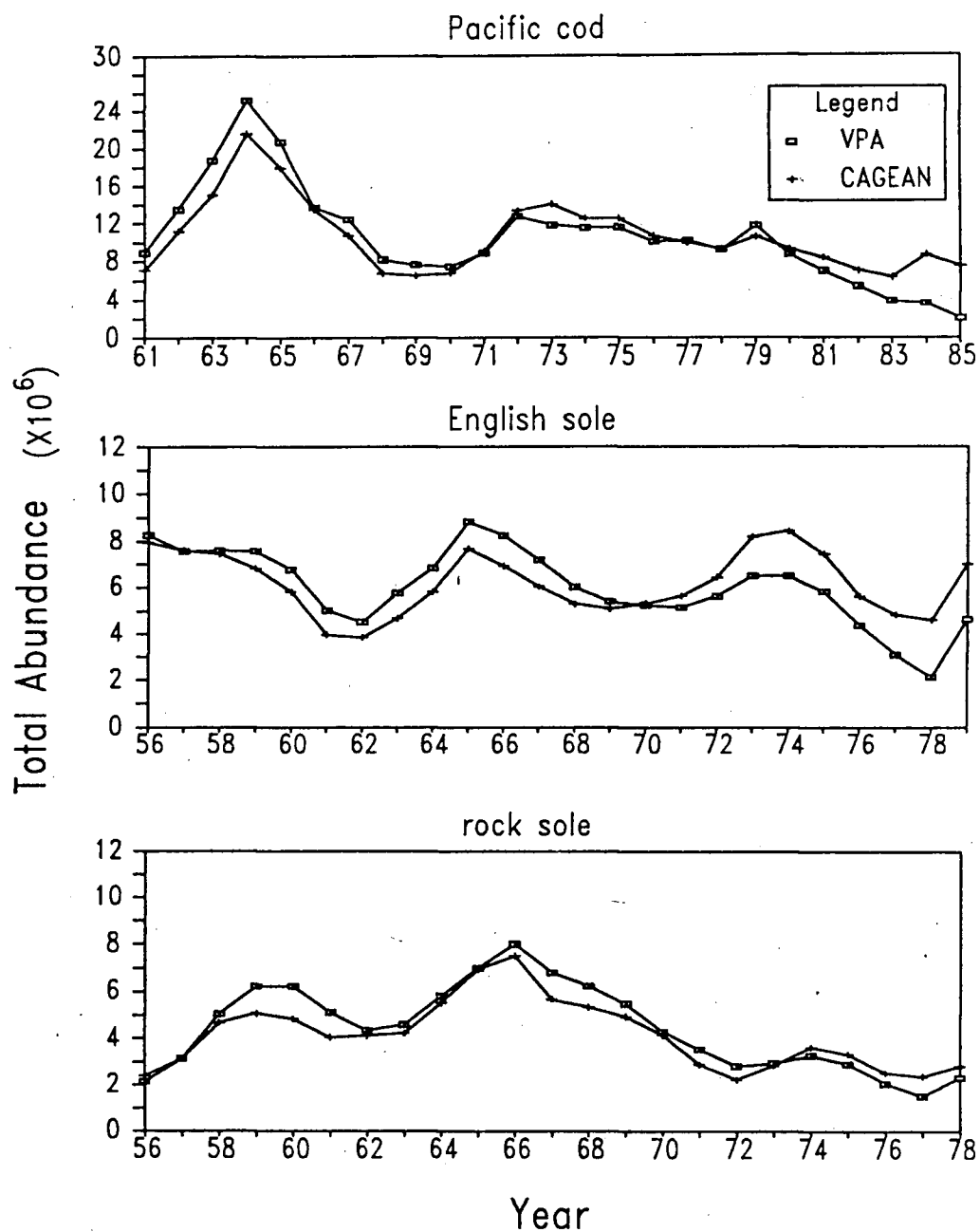


Figure 7.4. Estimates of total abundance of Pacific cod (ages 2-10), English sole (females ages 3-17) and rock sole (females ages 4-15 and northern stock only) in Hecate Strait obtained from VPA and CAGEAN using best estimates of input parameters. Note: The legend in the plot for Pacific cod applies to all three species.

The abundances of English sole and rock sole females are similar in magnitude and show very similar time trends (Fig. 7.4). Peaks in English sole abundance occurred in the late 1950's, 1965 and 1974, and troughs occurred in 1962 and 1971. Peaks and troughs in rock sole abundance appear to lag about 1 year behind the peaks and troughs in English sole abundance. As with cod, the causes of the cyclical trends in abundance of the two flatfish species are unknown, but recruitment of rock sole is positively correlated with water temperature (Fargo 1985).

Patterns in VPA and CAGEAN estimates of catchability coefficients were similar to abundance estimates (Fig. 7.5). Cod catchability coefficients were generally smaller than catchability coefficients for either of the flatfish. Peaks of cod catchability occurred in 1962, 1966 (VPA; 1967 CAGEAN) 1973, and 1983 (CAGEAN) and troughs occurred in 1964 (VPA; 1965 CAGEAN), 1968 (VPA; 1970 CAGEAN), 1974 (VPA), and 1980 (VPA; 1978 CAGEAN; Fig. 7.5). The estimated catchability of English sole shows a major peak in 1960, and minor peaks in 1970 and 1975. Troughs in English sole catchability occurred in 1966 and 1974 (VPA; 1972 CAGEAN) (Fig. 7.5). Rock sole catchability estimates fluctuated rather violently in the first two thirds (i.e. 1956-69) of the time series, when peaks occurred in 1958, 1961 and 1967 and troughs occurred in 1959, 1965, 1969 (VPA; 1968 CAGEAN). Fluctuations in estimated catchability of rock sole are damped in the latter part of the time series (i.e. 1970-1977) with peaks in 1970-71, and 1975 and a trough in 1974 (Fig. 7.5).

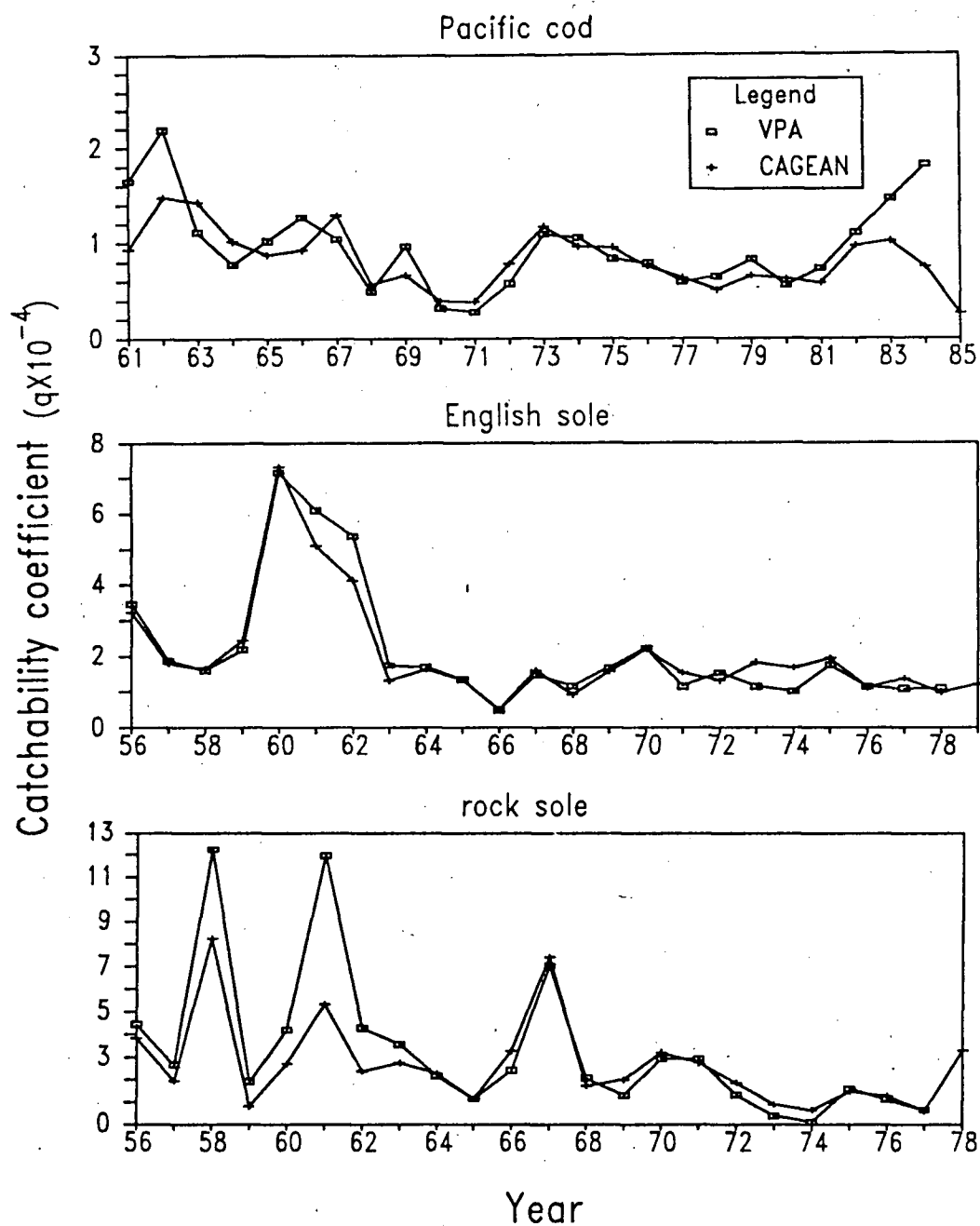


Figure 7.5. Estimates of catchability coefficients for Pacific cod (ages 4-10), English sole (ages 6-10) and rock sole (ages 6-10) obtained from VPA and CAGEAN using best estimates of input parameters. Note: The legend in the plot for Pacific cod applies to all three species.

Sensitivity Analyses - VPA

Alternative M Values

Estimates of abundance for the three species obtained from VPA using M_B , $M_B+50\%$, and $M_B-50\%$ are presented in figure 7.6. Abundance estimates were greater for $M_B+50\%$ and less for $M_B-50\%$ than for M_B for all three species (Fig. 7.6). However, within species abundance estimates for all M values were highly correlated (Table 7.1). Thus, while the use of different M values affected the magnitude of abundance estimates, it resulted in similar time trends (Fig. 7.6).

Catchability estimates were generally less affected by alternative M values than abundance estimates because catchabilities were estimated for fully recruited ages only, and therefore they were not affected by the abundance estimates for younger ages that are more biased when M is incorrect (Lapointe et al. 1989; Fig. 7.7). Catchability estimates were less for $M_B+50\%$ and greater for $M_B-50\%$ than for M_B for all three species (Fig. 7.7) because for any given year the abundance and catchability are inversely proportional to each other (i.e. via eq. 7.14). As with abundance estimates, within species estimates of catchability for all M values were highly correlated (Table 7.2). Thus, the use of different M values resulted in similar time trends in the catchability estimates (Fig. 7.7). My results are consistent with past studies which have investigated errors in M (e.g. Agger et al. 1973; Bradford and Peterman 1989). However, I did not find different time trends in incomplete cohorts when different M values were used as documented by Bradford and Peterman (1989), because I used iterative VPA (Rivard 1983).

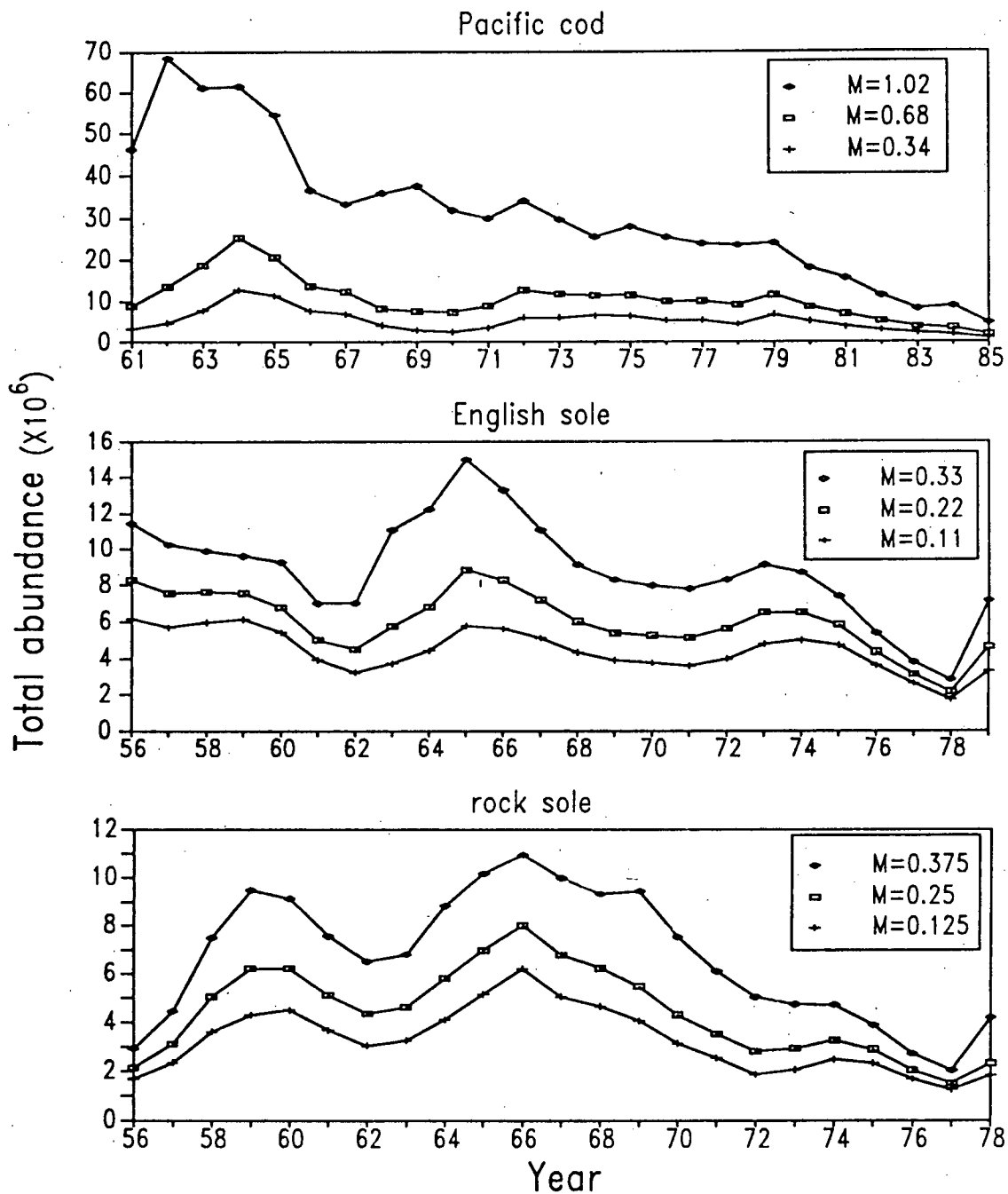


Figure 7.6. Estimates of total abundance of Pacific cod (ages 2-10), English sole (ages 3-17) and rock sole (ages 4-15) obtained from VPA using alternative M values. M values in legend for each species are $M_B + 50\%$ (top), M_B (middle) and $M_B - 50\%$ (bottom).

Table 7.1. Product-moment correlation matrices of abundance estimates obtained from VPA using alternative M values (M_B , $M_B+50\%$, and $M_B-50\%$) for Pacific cod, English sole and rock sole. Note: r 0.05, and r 0.01 are the values of the correlation coefficient necessary for significance at $P=0.05$ and $P=0.01$, respectively.

<i>Pacific cod</i>			
M value	r value		
0.68	1.0		
1.02	.81	1.0	
0.34	.95	.62	1.0
	0.68	1.02	0.34
n=25, df=23, r 0.05 = 0.40, r 0.01 = 0.50			
<i>English sole</i>			
M value	r value		
0.22	1.0		
0.33	.92	1.0	
0.11	.96	.78	1.0
	0.22	0.33	0.11
n=24, df=22, r 0.05 = 0.40, r 0.01 = 0.52			
<i>rock sole</i>			
M value	r value		
0.25	1.0		
0.375	.98	1.0	
0.125	.99	.96	1.0
	0.25	0.375	0.125
n=23, df=21, r 0.05 = 0.41, r 0.01 = 0.53			

Alternative Terminal q Values

The choice of alternative terminal q values had very little affect on magnitude of estimates of abundances or catchability coefficients for any of the three species (Figs. 7.8, 7.9), and within species estimates from the three

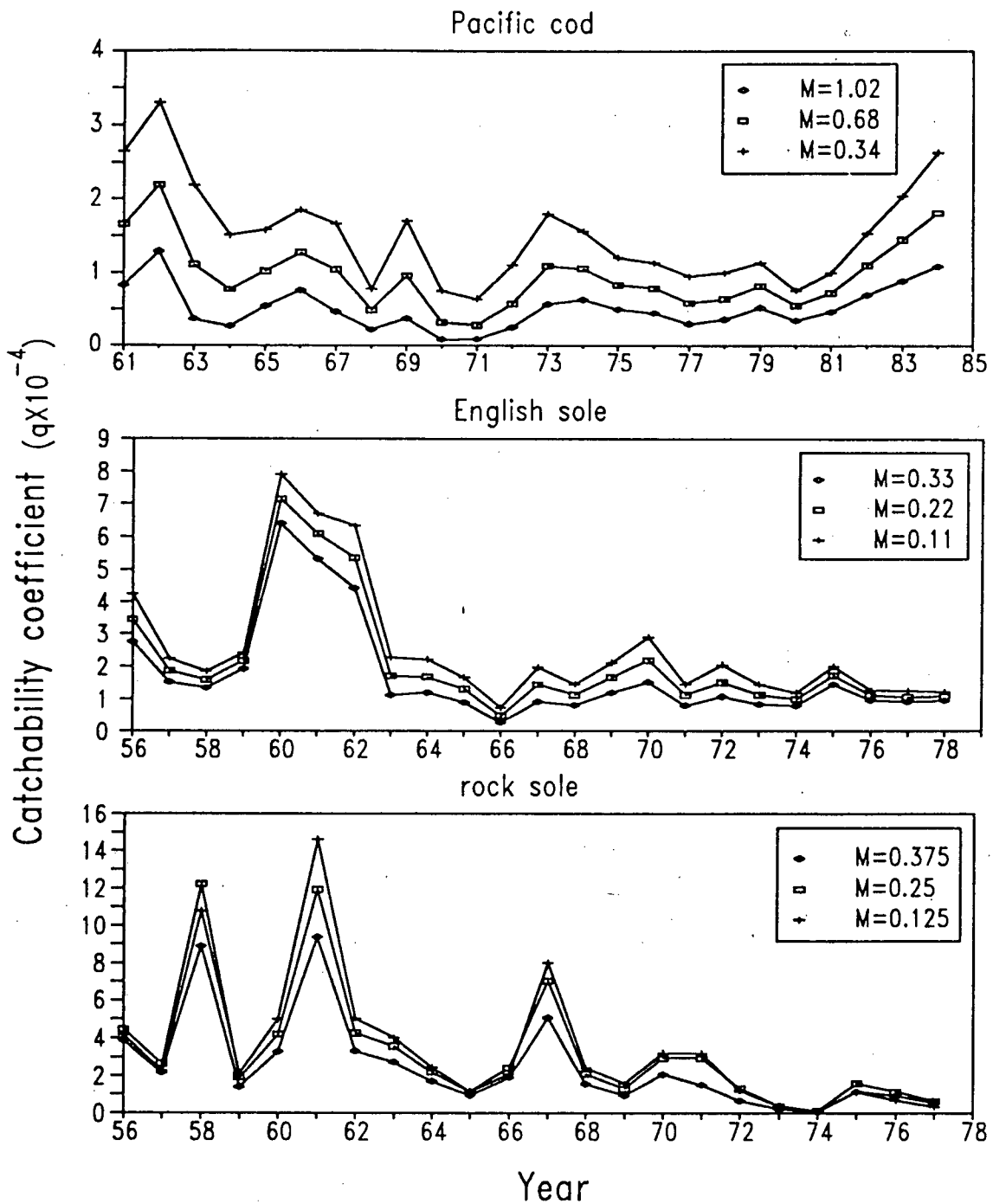


Figure 7.7. Estimates of catchability coefficients for Pacific cod (ages 4-10), English sole (ages 6-10) and rock sole (ages 6-10) obtained from VPA using alternative M values. M values in legend for each species are $M_B + 50\%$ (top), M_B (middle) and $M_B - 50\%$ (bottom).

Table 7.2. Product-moment correlation matrices of catchability estimates obtained from VPA using alternative M values (M_B , $M_B + 50\%$, and $M_B - 50\%$) for Pacific cod, English sole and rock sole.

<i>Pacific cod</i>				
M value	r value			
0.68	1.0			
1.02	.95	1.0		
0.34	.97	.86	1.0	
	0.68	1.02	0.34	
n=24, df=22, $r_{0.05} = 0.40$, $r_{0.01} = 0.52$				
<i>English sole</i>				
M value	r value			
0.22	1.0			
0.33	1.0	1.0		
0.11	1.0	.99	1.0	
	0.22	0.33	0.11	
n=23, df=21, $r_{0.05} = 0.41$, $r_{0.01} = 0.53$				
<i>rock sole</i>				
M value	r value			
0.25	1.0			
0.375	1.0	1.0		
0.125	.98	.98	1.0	
	0.25	0.375	0.125	
n=22, df=20, $r_{0.05} = 0.42$, $r_{0.01} = 0.54$				

alternative q values were very highly correlated (all $r_s > 0.99$, $P < 0.01$). I found little affect of the choice of alternative q values because these values only enter into the VPA calculations in the estimation of the abundances of the oldest age class in each year (i.e. N_t s in eq. 7.5) and in almost all years the catches of the oldest age class (i.e. C_t s in eq. 7.5; C_A s in Fig. 7.3) are zero for all three species (see Appendix A; Tables A1-A3). Thus, regardless of the choice of terminal q value, the estimate of abundance of the oldest age class will also be

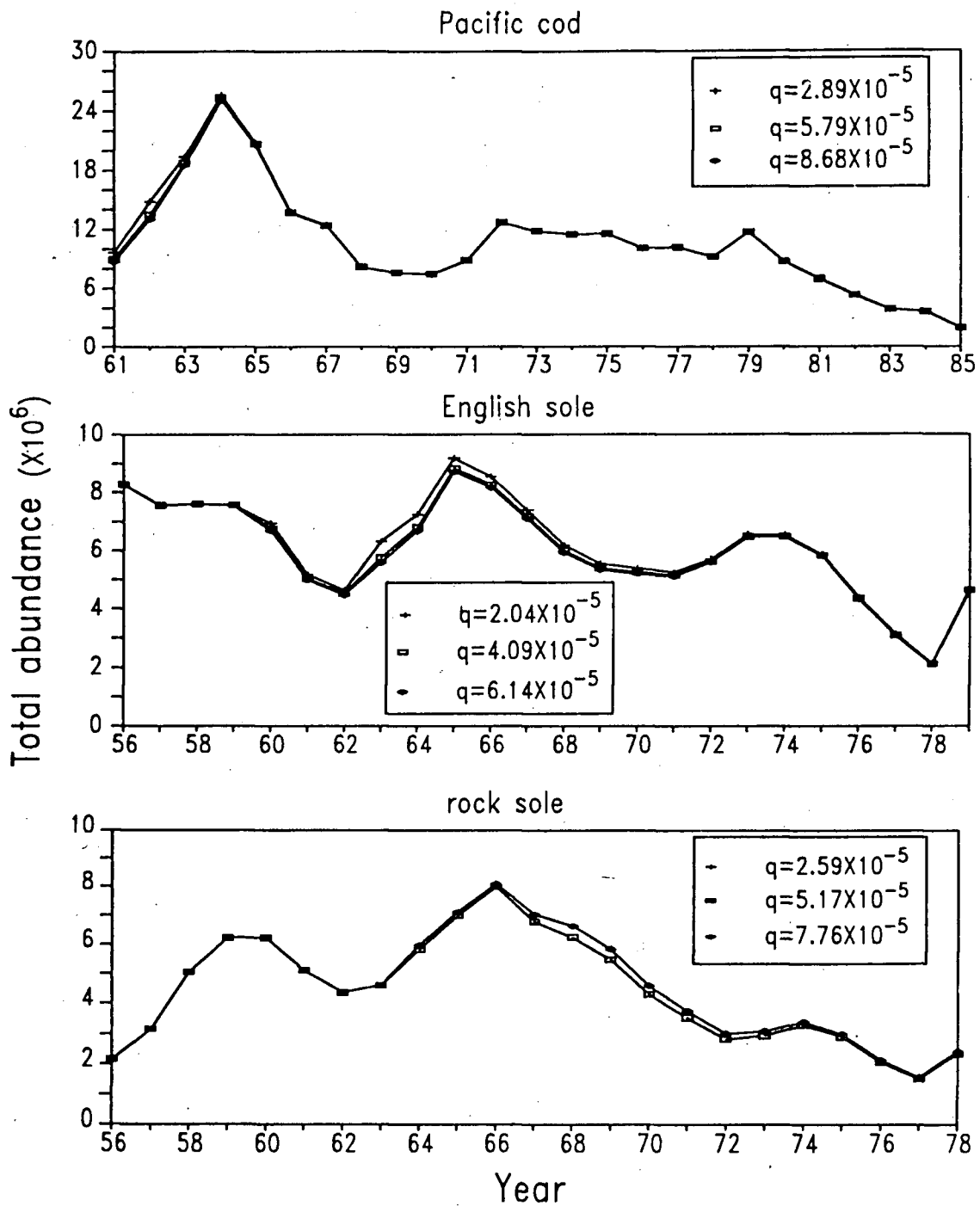


Figure 7.8. Estimates of total abundance of Pacific cod (ages 2-10), English sole (ages 3-17) and rock sole (ages 4-15) obtained from VPA using alternative terminal q values. The q values in legend for each species are $q_B + 50\%$ (top), q_B (middle) and $q_B - 50\%$ (bottom).

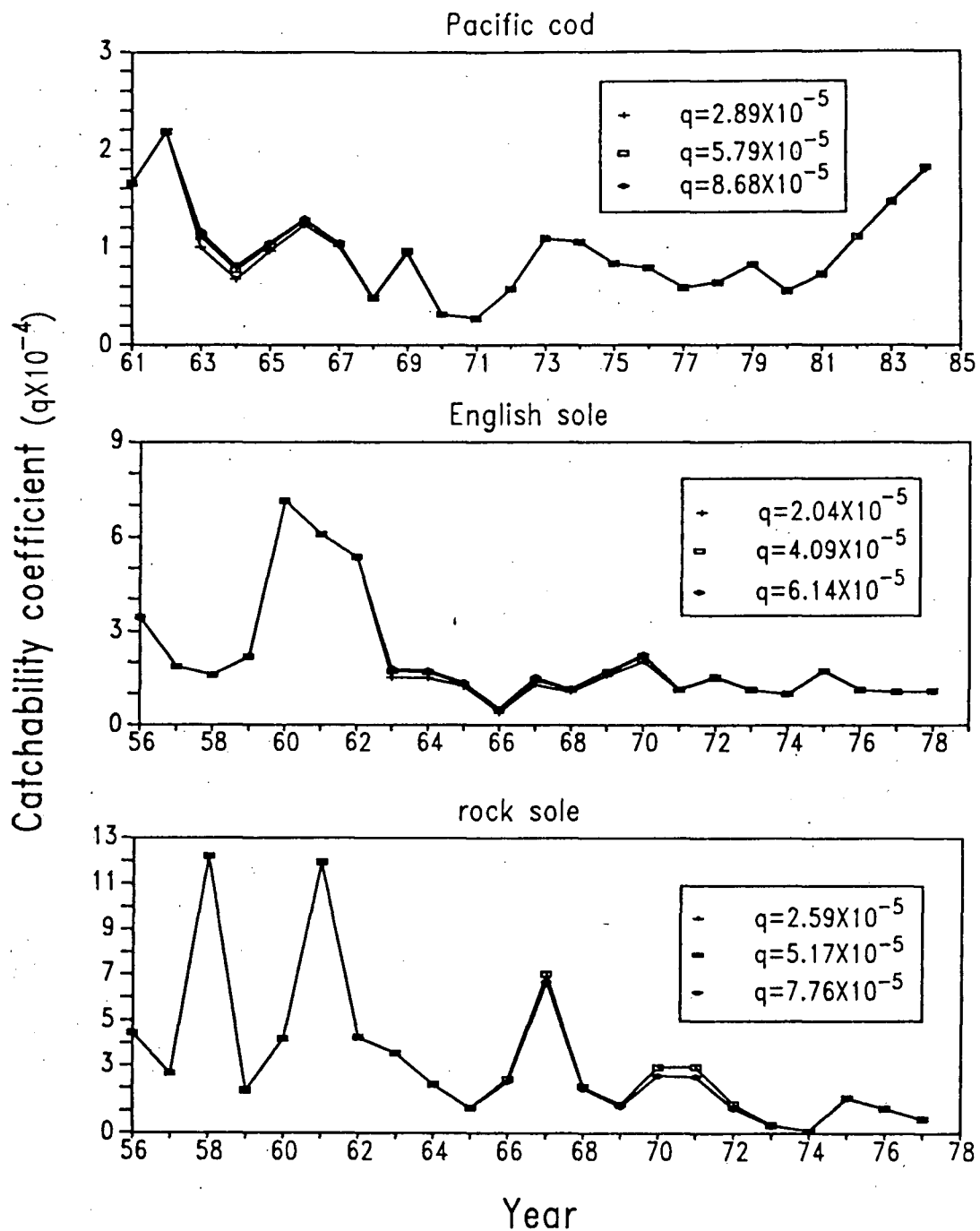


Figure 7.9. Estimates of catchability coefficients for Pacific cod (ages 4-10), English sole (ages 6-10) and rock sole (ages 6-10) obtained from VPA using alternative terminal q values. The q values in legend for each species are $q_B + 50\%$ (top), q_B (middle) and $q_B - 50\%$ (bottom).

zero. These results are consistent with Pope (1972) who found that VPA abundance estimates are insensitive to the choice of terminal fishing mortality when cumulative fishing mortality on the cohort is large because large cumulative fishing mortality results in few fish surviving to, and being caught in, the oldest age class.

Sensitivity Analyses - CAGEAN

Alternative M Values

The affect of alternative M values on CAGEAN abundance estimates was similar to that found for VPA estimates; abundance estimates were greater for $M_B + 50\%$ and less for $M_B - 50\%$ than for M_B for all three species (Fig. 7.10), and within species estimates for all M values were highly correlated (Table 7.3). Thus, the use of different M values resulted in similar time trends in the CAGEAN abundance estimates (Fig. 7.10).

CAGEAN catchability estimates (Fig. 7.11) were generally less affected by alternative M values than abundance estimates because catchability estimates were not affected by abundance estimates for partially recruited younger ages which are more biased when M is incorrect (Lapointe et al. 1989). Catchability estimates were less for $M_B + 50\%$ and greater for $M_B - 50\%$ than for M_B for all three species (Fig. 7.11) because for any given year abundance and fishing mortality are negatively correlated (i.e. via eq. 7.4) and fishing mortality is proportional to catchability (i.e. via eq. 7.15). As with abundance estimates, within species estimates of catchability for all M values were highly correlated (Table 7.4), and different M values resulted in similar time trends in the catchability estimates.

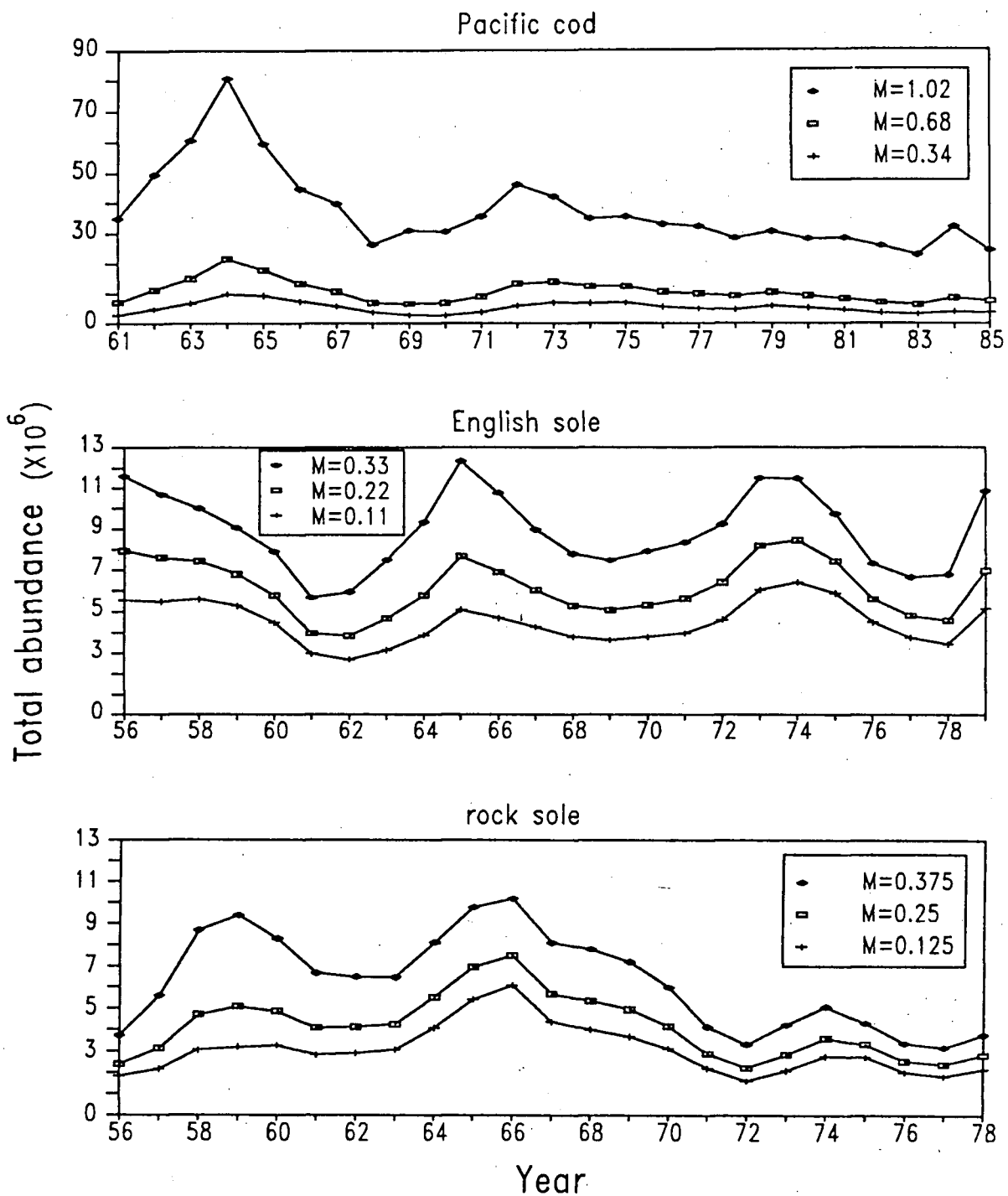


Figure 7.10. Estimates of total abundance of Pacific cod (ages 2-10), English sole (ages 3-17) and rock sole (ages 4-15) obtained from CAGEAN using alternative M values. M values in legend for each species are $M_B + 50\%$ (top), M_B (middle) and $M_B - 50\%$ (bottom).

Table 7.3. Product-moment correlation matrices of abundance estimates obtained from CAGEAN using alternative M values (M_B , $M_B+50\%$, and $M_B-50\%$) for Pacific cod, English sole and rock sole.

<i>Pacific cod</i>			
M value	r value		
0.68	1.0		
1.02	.91	1.0	
0.34	.96	.78	1.0
	0.68	1.02	0.34
n=25, df=23, r 0.05 = 0.40, r 0.01 = 0.50			
<i>English sole</i>			
M value	r value		
0.22	1.0		
0.33	1.0	1.0	
0.11	1.0	.99	1.0
	0.22	0.33	0.11
n=24, df=22, r 0.05 = 0.40, r 0.01 = 0.51			
<i>rock sole</i>			
M value	r value		
0.25	1.0		
0.375	.95	1.0	
0.125	.98	.87	1.0
	0.25	0.375	0.125
n=23, df=21, r 0.05 = 0.41, r 0.01 = 0.53			

Alternative Terminal F Values

The magnitude of, and trends in, CAGEAN estimates of abundances or catchability coefficients for all the three species were insensitive to the choice of terminal F values (Figs. 7.12, 7.13; all $r_s > 0.99$, $P < 0.01$). However, the underlying reason for the lack of effect of alternative F values on CAGEAN estimates is different from that for VPA estimates. Recall that the alternative

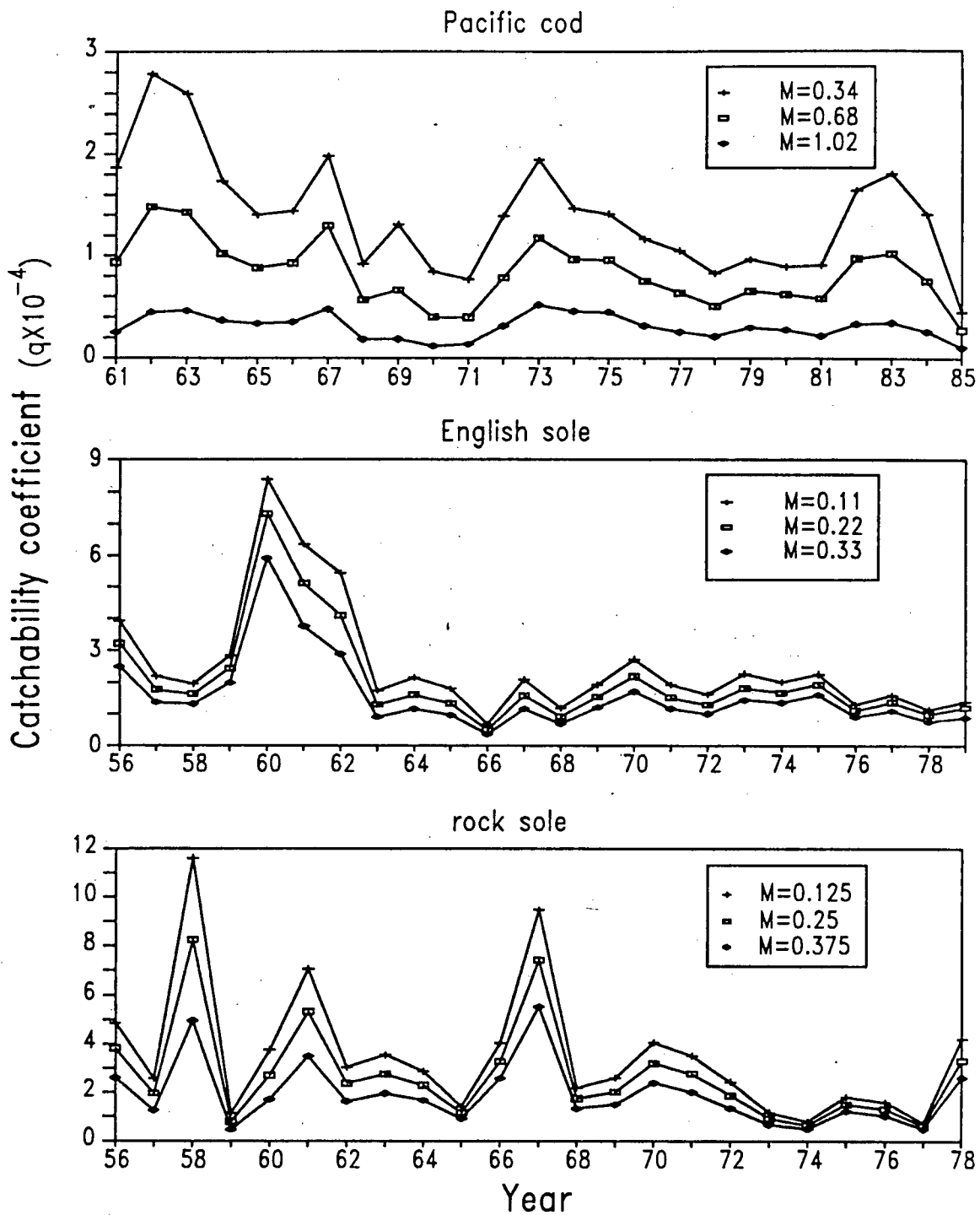


Figure 7.11. Estimates of catchability coefficients for Pacific cod (ages 4-10), English sole (ages 6-10) and rock sole (ages 6-10) obtained from CAGEAN using alternative M values. M values in legend for each species are $M_B + 50\%$ (top), M_B (middle) and $M_B - 50\%$ (bottom).

Table 7.4. Product-moment correlation matrices of catchability estimates obtained from CAGEAN using alternative M values (M_B , $M_B+50\%$, and $M_B-50\%$) for Pacific cod, English sole and rock sole.

<i>Pacific cod</i>			
M value	r value		
0.68	1.0		
1.02	.90	1.0	
0.34	.97	.78	1.0
	0.68	1.02	0.34
n=25, df=23, r 0.05 = 0.40, r 0.01 = 0.50			
<i>English sole</i>			
M value	r value		
0.22	1.0		
0.33	1.0	1.0	
0.11	1.0	.98	1.0
	0.22	0.33	0.11
n=24, df=22, r 0.05 = 0.40, r 0.01 = 0.51			
<i>rock sole</i>			
M value	r value		
0.25	1.0		
0.375	.99	1.0	
0.125	1.0	.97	1.0
	0.25	0.375	0.125
n=23, df=21, r 0.05 = 0.41, r 0.01 = 0.53			

terminal F values were used in CAGEAN's routine called COHORT which calculated alternative starting parameters for the nonlinear estimation. Thus, CAGEAN estimates were insensitive to the choice of terminal F values because the nonlinear estimation converged on nearly identical parameter estimates over the range of alternative input parameters generated by $F_B \pm 50\%$. Thus, unlike VPA, CAGEAN is robust to the choice of terminal F value regardless of the cumulative fishing mortality on cohorts, unless these terminal F values are

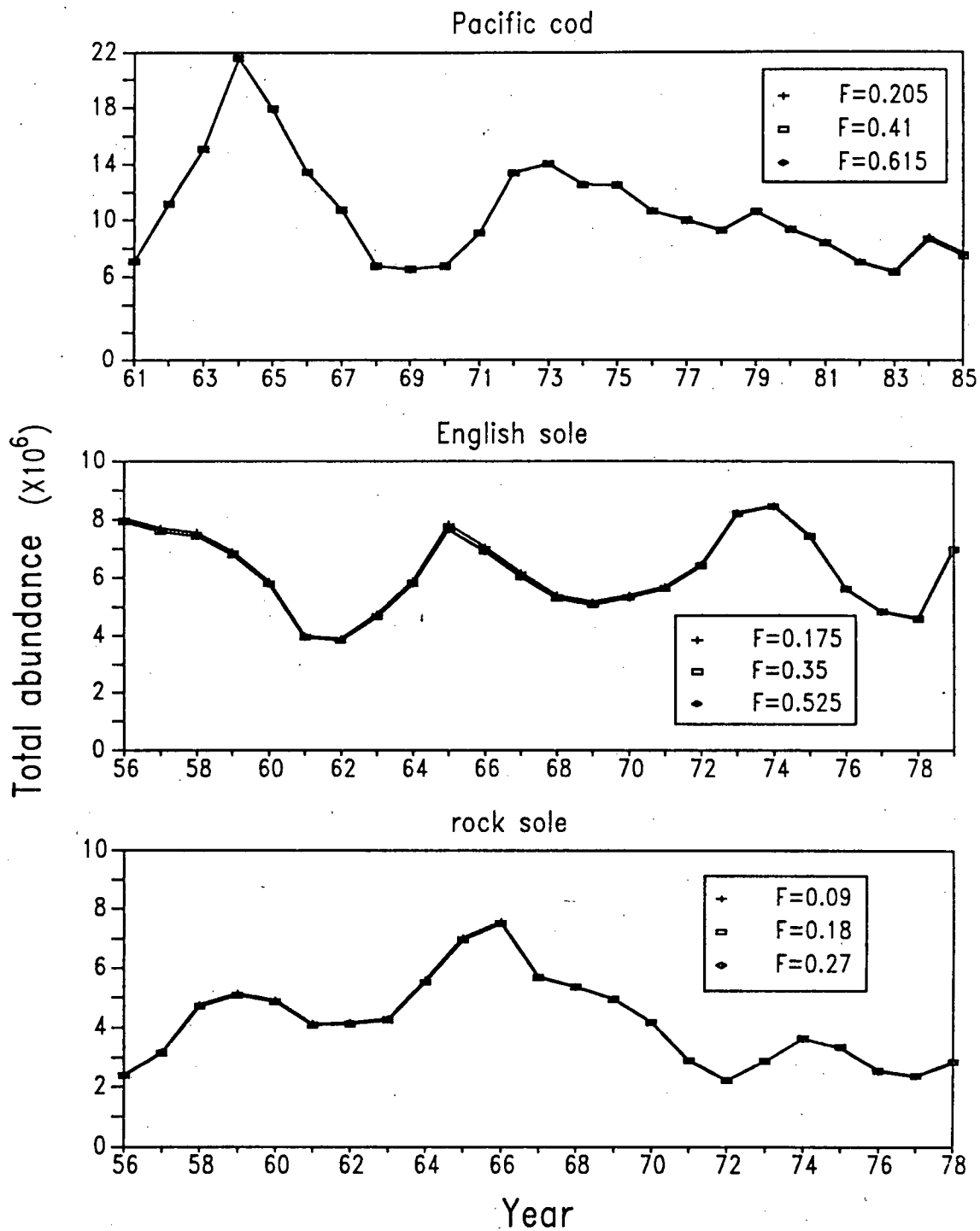


Figure 7.12. Estimates of total abundance of Pacific cod (ages 2-10), English sole (ages 3-17) and rock sole (ages 4-15) obtained from CAGEAN using alternative F values. F values in legend for each species are $F_B + 50\%$ (top), F_B (middle) and $F_B - 50\%$ (bottom).

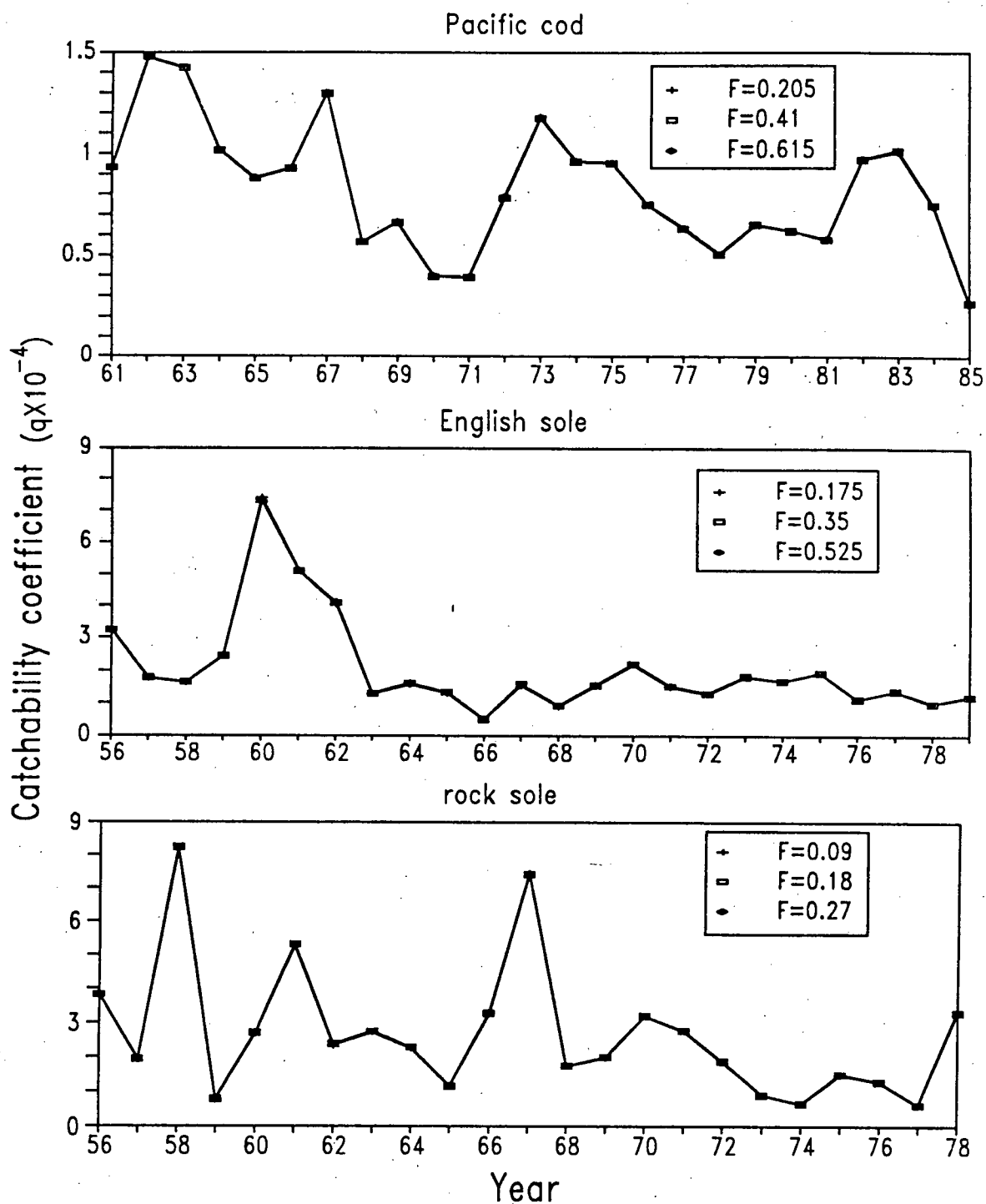


Figure 7.13. Estimates of catchability coefficients for Pacific cod (ages 4-10), English sole (ages 6-10) and rock sole (ages 6-10) obtained from CAGEAN using alternative F values. F values in legend for each species are $F_B + 50\%$ (top), F_B (middle) and $F_B - 50\%$ (bottom).

different enough to cause the nonlinear estimation to converge on different local minima.

Alternative λ Values

Cagean estimates of abundances obtained from the five alternative λ values combination are shown in figure 7.14. The magnitude of, and trends in abundance estimates were generally insensitive to the range of λ value combinations examined with the exception of $\lambda_1=\lambda_2=100$ for all three species and $\lambda_1=\lambda_2=0$ for the two flatfish species (Fig. 7.14; Table 7.5). The use of $\lambda_1=\lambda_2=100$ resulted in greatly damped fluctuations in abundance for all three species in comparison to other λ value combinations (Fig. 7.14). Abundance estimates obtained when $\lambda_1=\lambda_2=0.5$ were intermediate in magnitude for all three species compared to estimates obtained using other λ value combinations (Fig. 7.14).

Cod abundance estimates were least sensitive to the range of λ values explored (Fig. 7.14); estimates from all λ combinations were highly correlated; all r s > 0.70, $P < 0.01$; Table 7.5). Flatfish abundance estimates were unrealistically high later in the time series when $\lambda_1=\lambda_2=0$ (Fig. 7.14). Furthermore, these estimates were not significantly correlated with estimates from other λ value combinations in either species, with the exception that rock sole estimates for $\lambda_1=\lambda_2=0$ were significantly negatively correlated with estimates obtained when $\lambda_1=\lambda_2=100$ (Table 7.5). Intermediate weights on auxiliary data (i.e. $\lambda_1=\lambda_2=0.5$, $\lambda_1=1$, $\lambda_2=0$, or $\lambda_1=0$, $\lambda_2=1$) yielded estimates that were very highly correlated for both flatfish species (all r s > 0.96, $P < 0.01$ for English sole; all r s > 0.89, $P < 0.01$ for rock sole; Table 7.5).

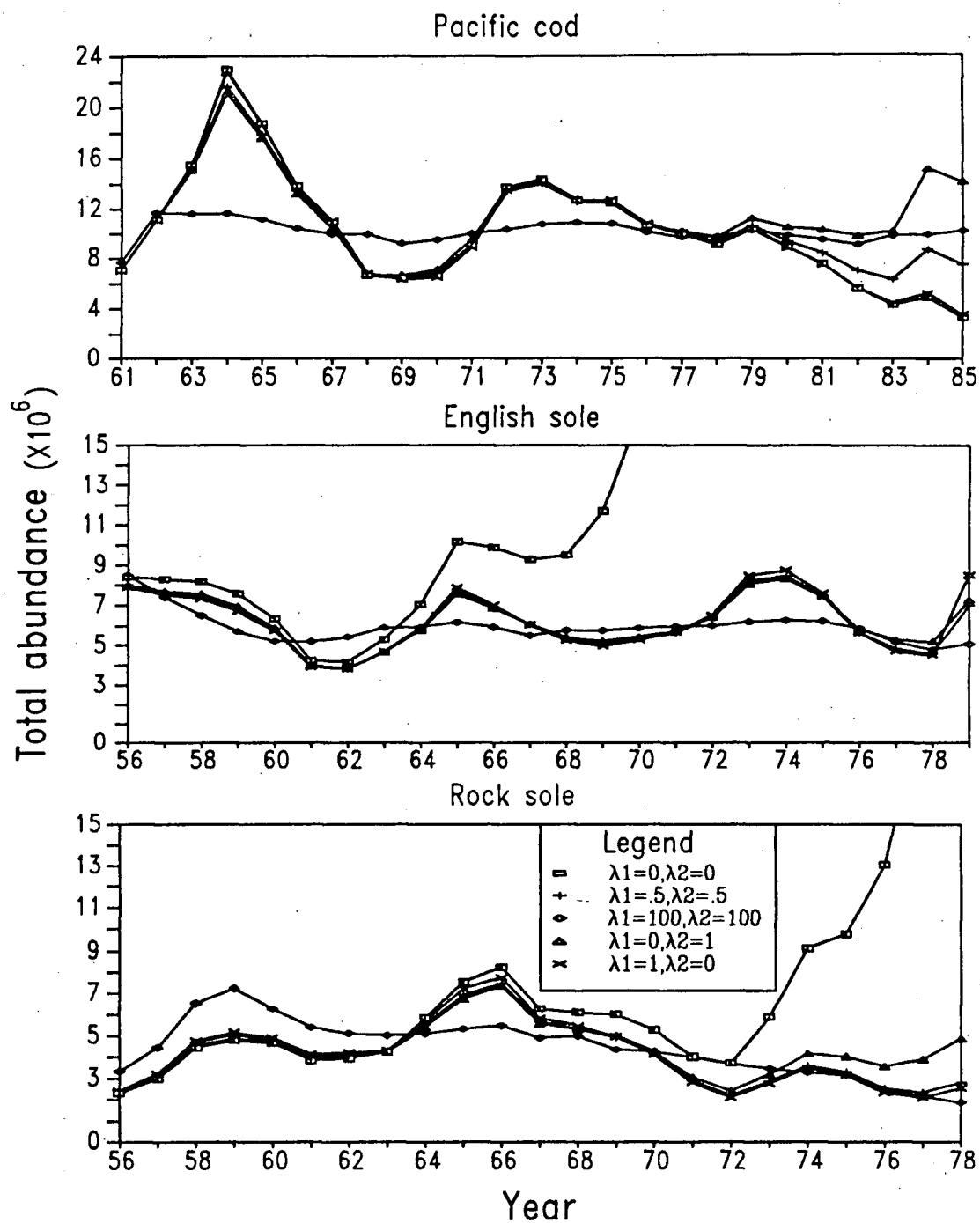


Figure 7.14. Estimates of total abundance of Pacific cod (ages 2-10), English sole (ages 3-17) and rock sole (ages 4-15) obtained from CAGEAN using alternative λ values. Note: Legend in plot for rock sole applies to all species.

Table 7.5. Product-moment correlation matrices of abundance estimates obtained from CAGEAN using alternative λ values for Pacific cod, English sole and rock sole.

<i>Pacific cod</i>					
λ value	<i>r</i> value				
$\lambda_1, \lambda_2 = 0$	1.0				
$\lambda_1, \lambda_2 = 0.5$.97	1.0			
$\lambda_1, \lambda_2 = 100$.70	.76	1.0		
$\lambda_1 = 0, \lambda_2 = 1$.72	.86	.73	1.0	
$\lambda_1 = 1, \lambda_2 = 0$	1.0	.98	.71	.73	1.0
	$\lambda_1, \lambda_2 = 0$	$\lambda_1, \lambda_2 = 0.5$	$\lambda_1, \lambda_2 = 100$	$\lambda_1 = 0, \lambda_2 = 1$	$\lambda_1 = 1, \lambda_2 = 0$
n=25, df=23, <i>r</i> 0.05 = 0.40, <i>r</i> 0.01 = 0.50					

<i>English sole</i>					
λ value	<i>r</i> value				
$\lambda_1, \lambda_2 = 0$	1.0				
$\lambda_1, \lambda_2 = 0.5$.05	1.0			
$\lambda_1, \lambda_2 = 100$	-.35	.62	1.0		
$\lambda_1 = 0, \lambda_2 = 1$.11	.99	.60	1.0	
$\lambda_1 = 1, \lambda_2 = 0$.24	.98	.53	.97	1.0
	$\lambda_1, \lambda_2 = 0$	$\lambda_1, \lambda_2 = 0.5$	$\lambda_1, \lambda_2 = 100$	$\lambda_1 = 0, \lambda_2 = 1$	$\lambda_1 = 1, \lambda_2 = 0$
n=24, df=22, <i>r</i> 0.05 = 0.40, <i>r</i> 0.01 = 0.51					

<i>rock sole</i>					
λ value	<i>r</i> value				
$\lambda_1, \lambda_2 = 0$	1.0				
$\lambda_1, \lambda_2 = 0.5$	-.24	1.0			
$\lambda_1, \lambda_2 = 100$	-.60	.69	1.0		
$\lambda_1 = 0, \lambda_2 = 1$.15	.92	.43	1.0	
$\lambda_1 = 1, \lambda_2 = 0$	-.27	1.0	.71	.90	1.0
	$\lambda_1, \lambda_2 = 0$	$\lambda_1, \lambda_2 = 0.5$	$\lambda_1, \lambda_2 = 100$	$\lambda_1 = 0, \lambda_2 = 1$	$\lambda_1 = 1, \lambda_2 = 0$
n=23, df=21, <i>r</i> 0.05 = 0.41, <i>r</i> 0.01 = 0.53					

The unrealistically high abundance estimates found for flatfish when no auxiliary data were used are consistent with previous studies (e.g. Doubleday 1976; Pope 1977; Deriso et al. 1985) that showed how catch-at-age data alone give unstable estimates. The problem is particularly acute later in the time series when cohorts are incomplete, because there are fewer catch-at-age observations per cohort.

Large λ values resulted in damped fluctuations in abundance estimates in all three species for three reasons. First, when λ_1 is large, CAGEAN predicts that q is constant because a large penalty is attached to effort residuals in equation 7.11. Second, with a constant q , fluctuations in F_t s depend solely on fluctuations in E_t s yet effort has not fluctuated that much for any of the species over the data series. Thus, the F_t s are relatively constant and moderate for all species (i.e. average $F=0.46 \pm 0.05\text{SE}$ for cod; $0.46 \pm 0.06\text{SE}$ for English sole; $0.38 \pm 0.06\text{SE}$ for rock sole). Third, when λ_2 is large, recruitment is a deterministic function of spawning stock because of the large penalty attached to spawner-recruit residuals in equation 7.13 and fluctuations in recruitment due to spawning stock variations are relatively small. Thus, when λ_1 and λ_2 are large, CAGEAN generates abundance estimates that are the same as would be predicted from a deterministic population model with moderate exploitation rates.

The patterns in the sensitivity of catchability estimates were similar to those found for abundances (Fig. 7.15). Catchability estimates obtained when $\lambda_1 = \lambda_2 = 0.5$ were intermediate in magnitude for all three species compared to estimates for other λ value combinations. When $\lambda_1 = \lambda_2 = 100$, estimates of catchability coefficients were nearly constant for all years and species. Constant catchability is expected when λ_1 is large because under such conditions CAGEAN converges to the constant catchability model of Paloheimo (1980; Deriso et al.

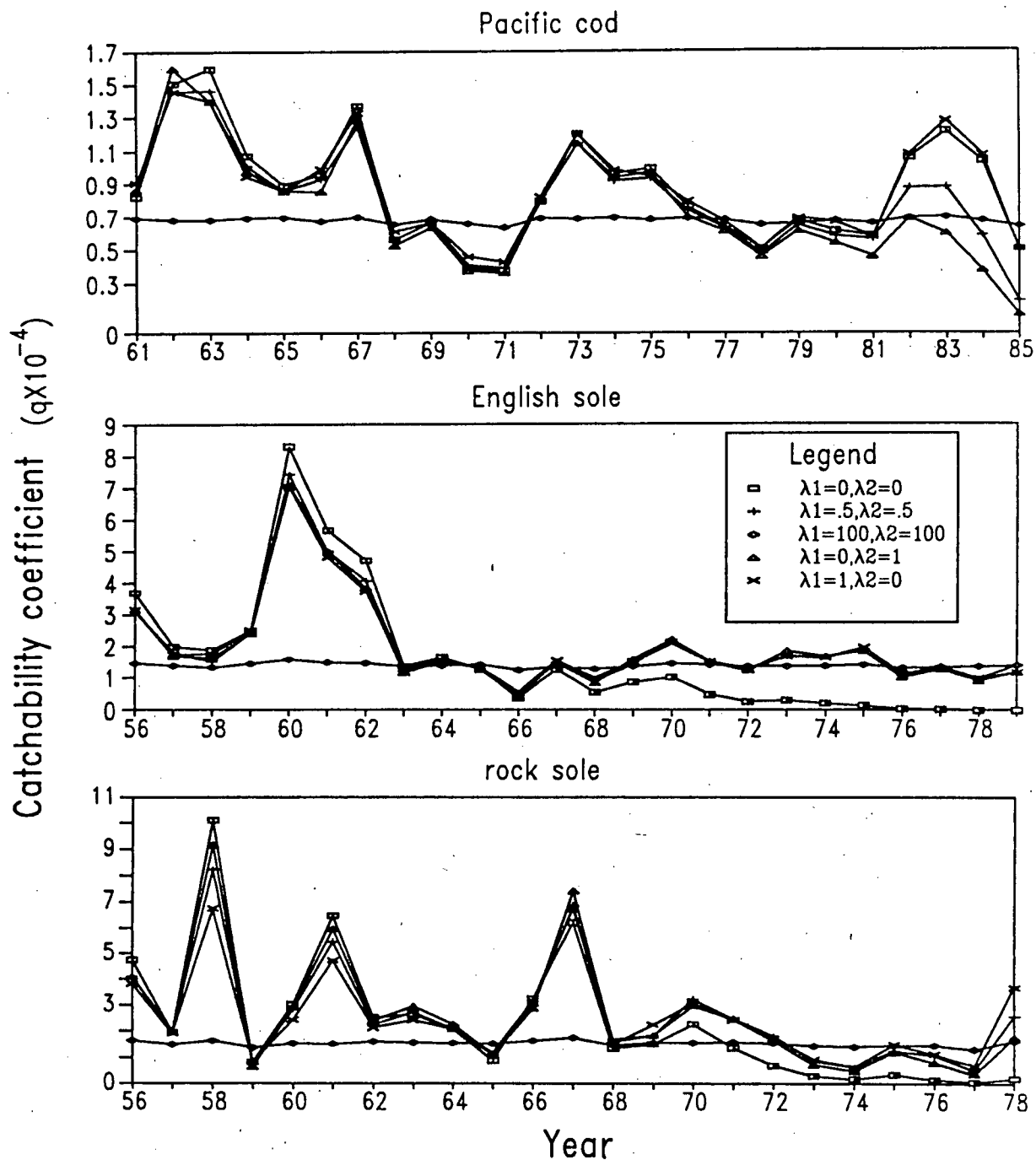


Figure 7.15. Estimates of catchability coefficients for Pacific cod (ages 4-10), English sole (ages 6-10) and rock sole (ages 6-10) obtained from CAGEAN using alternative λ values. Note: Legend in plot for English sole applies to all species.

1985).

Cod catchability estimates for all λ value combinations except the constant catchability model (i.e. $\lambda_1 = \lambda_2 = 100$) were highly correlated (all $r_s > 0.81$, $P < 0.01$; Table 7.6). The estimates of catchability coefficients for both flatfish species were unrealistically low during the years that abundance estimates were unrealistically high because of the negative correlation between abundance estimates and fishing mortalities (hence q 's; Figs. 7.14 and 7.15). However, English sole catchabilities estimated from all λ value combinations were highly correlated ($r \geq 0.79$, $P < 0.01$; Table 7.6). Correlations among rock sole catchability estimates obtained from different λ value combinations were lowest for $\lambda_1 = \lambda_2 = 100$ and highest for intermediate λ values (all $r_s \geq 0.89$, $P < 0.01$; Table 7.6).

In summary, estimates of abundances and catchabilities were generally not sensitive to the alternative λ value combinations when intermediate values were used. Catchability and abundances estimates obtained when $\lambda_1 = \lambda_2 = 0.5$ were intermediate compared to estimates obtained from other λ values.

Comparison of Estimates from VPA and CAGEAN

Estimates of abundances and catchabilities obtained from VPA and CAGEAN using the best parameter estimates were generally very similar (Figs. 7.4 and 7.5). Cod abundance estimates from VPA were highly correlated with CAGEAN abundance estimates ($r = 0.92$, $p < 0.01$). Cod catchability estimates obtained from the two methods were less highly correlated than abundance estimates ($r = 0.68$, $P < 0.05$). Cod catchability estimates from the two techniques were particularly different early and late in the time series (Fig. 7.5).

Table 7.6. Product-moment correlation matrices of catchability estimates obtained from CAGEAN using alternative λ values for Pacific cod, English sole and rock sole.

<i>Pacific cod</i>					
λ value	<i>r</i> value				
$\lambda_1, \lambda_2 = 0$	1.0				
$\lambda_1, \lambda_2 = 0.5$.93	1.0			
$\lambda_1, \lambda_2 = 100$.67	.69	1.0		
$\lambda_1 = 0, \lambda_2 = 1$.85	.97	.63	1.0	
$\lambda_1 = 1, \lambda_2 = 0$.99	.91	.70	.82	1.0
	$\lambda_1, \lambda_2 = 0$	$\lambda_1, \lambda_2 = 0.5$	$\lambda_1, \lambda_2 = 100$	$\lambda_1 = 0, \lambda_2 = 1$	$\lambda_1 = 1, \lambda_2 = 0$
n=25, df=23, <i>r</i> 0.05 = 0.40, <i>r</i> 0.01 = 0.50					

<i>English sole</i>					
λ value	<i>r</i> value				
$\lambda_1, \lambda_2 = 0$	1.0				
$\lambda_1, \lambda_2 = 0.5$.95	1.0			
$\lambda_1, \lambda_2 = 100$.79	.88	1.0		
$\lambda_1 = 0, \lambda_2 = 1$.95	1.0	.88	1.0	
$\lambda_1 = 1, \lambda_2 = 0$.95	1.0	.88	1.0	1.0
	$\lambda_1, \lambda_2 = 0$	$\lambda_1, \lambda_2 = 0.5$	$\lambda_1, \lambda_2 = 100$	$\lambda_1 = 0, \lambda_2 = 1$	$\lambda_1 = 1, \lambda_2 = 0$
n=24, df=22, <i>r</i> 0.05 = 0.40, <i>r</i> 0.01 = 0.51					

<i>rock sole</i>					
λ value	<i>r</i> value				
$\lambda_1, \lambda_2 = 0$	1.0				
$\lambda_1, \lambda_2 = 0.5$.96	1.0			
$\lambda_1, \lambda_2 = 100$.56	.69	1.0		
$\lambda_1 = 0, \lambda_2 = 1$.97	1.0	.66	1.0	
$\lambda_1 = 1, \lambda_2 = 0$.89	.98	.77	.96	1.0
	$\lambda_1, \lambda_2 = 0$	$\lambda_1, \lambda_2 = 0.5$	$\lambda_1, \lambda_2 = 100$	$\lambda_1 = 0, \lambda_2 = 1$	$\lambda_1 = 1, \lambda_2 = 0$
n=23, df=21, <i>r</i> 0.05 = 0.41, <i>r</i> 0.01 = 0.53					

English sole abundance estimates from VPA and CAGEAN were very similar ($r=0.66$, $P<0.05$), and catchability estimates obtained from the two techniques were highly correlated ($r=0.97$, $P<0.01$). Both catchability and abundance estimates obtained from the two methods were highly correlated for rock sole ($r=0.96$, $P<0.01$ for q ; $r=0.89$, $P<0.01$ for N).

Neither method was particularly more sensitive to alternative input parameters. The magnitude of estimates from both methods were sensitive to alternative M values but insensitive to alternative F values (CAGEAN; q values - VPA) for different reasons. In general, I would expect CAGEAN estimates to be least sensitive to alternative F values, particularly when auxiliary effort data are used, because CAGEAN is a non-sequential technique and F values are estimated from fits to the catch-at-age and effort data. Thus, errors in terminal F values do not propagate back through the cohorts in CAGEAN as they do in VPA.

Summary of Results and Conclusions

The sensitivity analyses have demonstrated that the magnitude of abundance and catchability estimates for all three species depends on the choice of M value (VPA & CAGEAN) and the λ values (CAGEAN only), but is insensitive to the choice of F_t values (CAGEAN) or q_t values (VPA). However, in most cases alternative input parameters resulted in abundance and catchability estimates that were highly correlated and had very similar time trends.

Thus, in the context of my analysis of functional responses which follows in chapter 8, it is unlikely that the use of abundance and catchability estimates obtained from alternative input parameters using either technique would result in

different qualitative forms of functional responses. However, because of the affect of alternative input parameters on the magnitude of abundance and catchability estimates obtained from VPA and CAGEAN, the magnitude of particular parameters for a given functional response model (e.g. α and β , in Fox's (1974) model) will depend on the mortality rates and/or λ values used. Therefore, my abilities to address specific quantitative consequences of functional responses are limited.

Similar temporal trends in abundance and catchability estimates were obtained from VPA and CAGEAN using the best estimates of input parameters, but the correlations were some what lower than those found for the sensitivity analyses for each method. Another source of potential differences in functional responses derived from abundance estimates using VPA and CAGEAN is that CAGEAN provides estimates of predicted catches. Thus in chapter 8, I will examine the implications of the alternative methods (i.e. VPA vs. CAGEAN) for the assessment of functional responses of trawlers in Hecate Strait.

Chapter 8: Functional Responses of Trawlers

Introduction

In this chapter I examine the functional responses of trawlers to the abundance of three species that are caught in a multispecies fishery located in Hecate Strait. Most of the examinations of functional responses in fisheries reviewed in Chapter 6 involved "single" species fisheries. One purpose of my study was to evaluate possible alternative functional response models and consider their implications in a multispecies situation. Thus, in order to put my research in perspective, I will briefly highlight the major areas of multispecies fisheries research before proceeding with further details on the present study. Many aspects of multispecies fisheries have been examined, and the investigations can be divided into four main categories.

First, a few studies have identified multispecies effort patterns by examining temporal and spatial patterns in species composition of catches (e.g. Tyler et al. 1984; Murawski et al. 1983; Biseau and Gondeaux 1988). The main purposes of these studies are to identify assemblages of species that could potentially be managed as a group (e.g. Tyler et al. 1982), or alternatively to identify subfleets for determining components of bioeconomic models (e.g. Biseau and Gondeaux 1988).

The second area of research concerns the development of techniques for determining the effort for single species that are caught with other species (e.g. Westrheim 1983; Stocker and Fournier 1984) or that compete with other species for space on (or in) fishing gear (e.g. Rothschild 1967). Single species effort is needed primary for calculation of abundance indices (i.e. LPE) that are commonly

the only available short term indicators of the response of a population to fishing.

Papers concerned with the multispecies assessment of fish populations fall into the third category. The impetus behind the development of these methods is that interactions among species (i.e. predation and competition; e.g. Sissenwine et al. 1982) may alter the growth and natural mortality rates of fish populations (particularly of younger ages classes) and therefore these interactions should be included in assessment models. Thus researchers have developed multispecies VPA models (e.g. Daan 1987) and multispecies yield per recruit models (e.g. Shepherd 1988). One of the drawbacks of multispecies models is that they require data that are often either unavailable or quite scarce (Ursin 1982).

The fourth category includes a variety of papers that investigate alternative harvest or management strategies for multispecies fisheries. This area of research can be divided into a few subcategories. One subcategory includes papers that consider the theoretical effects of species interactions on potential yields (e.g. Horwood 1976; Pope 1976). Another subarea of research investigates the theoretical implications of exploiting stocks or species with different sustainable harvest rates (e.g. Paulik et al. 1967; Hilborn 1976). A third subarea includes papers that use one of the multispecies assessment techniques or other techniques (e.g. linear programming) to consider alternative management options or to determine optimal policies for particular multispecies fisheries (e.g. Overholtz 1985; Murawski and Finn 1986; Pikitch 1987).

Despite the broad areas covered by multispecies research, there are very few studies that consider the responses of fishermen in a multispecies system, beyond a description of patterns in effort allocation among species (e.g. Tyler et

al. 1984). Specifically, one aspect that to my knowledge has not been investigated is the functional response of fishermen in a multispecies setting.

My investigation of functional responses has three main parts. Part 1 evaluates three alternative single species models for functional responses and mortality curves (e.g. Figs. 5.1 and 5.4) for each of the three species that are the major components of the multispecies fishery in Hecate Strait. Part 2 examines two multispecies functional response models that take into account the effects of the abundance of alternative prey on the functional response. Finally, in part 3, I present tests of Murdoch's (1969) switching hypothesis to examine a potential mechanism for generating type III functional responses by fishermen.

Data and Methods

Data Sets

In order to examine functional responses in the Hecate Strait trawl fishery, I required estimates of LPE (i.e. NA/T in the functional response equations of Chapter 5) and abundance for each of the three species. I used estimates of abundance obtained from VPA and CAGEAN using the "best" estimates of input parameters as presented in Chapter 7. For VPA, I estimated LPE by L/E where L is the total catch landed (i.e. estimated total numbers landed) and E is the total fishing effort (hours trawled) as described in Chapter 7 (see section "Data Preparation and Background Methods"). Note that hours trawled is analogous to pursuit time in a natural predator (i.e. T_p not T); it does not include time spent searching (while not trawling) for trawl sites, time spent moving between trawl sites or time spent handling catches. Hecate Strait trawlers may search some portion of the time while trawling because most of

the trawl sites are well known and some species, particularly flatfish are difficult to detect on the echo sounders. However, I do not expect to find evidence for handling time effects (i.e. saturation in the functional response), since handling time is not included in the effort measure. My main reason for choosing hours trawled allotted by species as the effort measure was that it is the effort measure used by fisheries biologist and managers and I wanted to consider the potential implications of functional responses on assessment and management. In order to maintain consistency between the catches and abundances obtained from CAGEAN, I used the catches predicted by equation 7.7 and the same effort data used for VPA to calculate the LPE for CAGEAN. In my fitting of the mortality curves (e.g. Figs. 5.4, 6.2b; catchability vs. abundance), I used estimates of catchability coefficients obtained from VPA (by eq. 7.14) and CAGEAN (by eq. 7.15).

In addition to using estimates obtained from the two catch-at-age methods, I also considered two age ranges for each species and method: (1) all fished ages and (2) fully recruited ages only. I examined functional responses for these two age ranges because the functional responses fit to data for all ages are affected by factors that change the partial recruitment of younger ages (e.g. density dependent growth). For example, if recruits were not completely vulnerable and fluctuations in abundance tended to be dominated by recruitment (as is common among exploited fish populations), then in years of large recruitment, abundance would be large and q would be small and vice versa for years of small recruitment. Thus, catchability would appear compensatory, but not because of the functional response of the predator. In contrast, the functional responses fit to data from the fully recruited age ranges should be determined more by factors underlying the dynamics of the functional response (e.g.

aggregation and switching). Thus for each species, I used a total of four data sets (2 age ranges \times 2 methods).

Alternative Single Species Models

I fit the three alternative models below to each of the four data sets for the three species:

$$1. \quad Y = aX \quad (8.1)$$

$$2. \quad Y = aX/(b + X) \quad (8.2)$$

$$3. \quad Y = aX/[X + b\exp(cX)] \quad (8.3)$$

where Y is LPE, X is abundance and, a , b and c are parameters to be estimated. Model 1 is a type I response without an asymptote. Model 2, the disc equation (i.e. equation 5.2, where $a = 1/t_h$ and $b = 1/at_h$), generates a type II response unless a and b are very large relative to X , in which case the response is linear with slope a/b . The third model is Fujii et al.'s (1978) generalized equation that can mimic response types I-IV. Model 3 is a rearrangement of equation 5.8b from Peterman (1980) where $Y = NA/T_p$, and the numerator and the denominator of the right hand side of 5.8b have been multiplied by N/t_h and where $a = 1/t_h$ and $b = 1/(dt_h)$.

Models 1-3 were used to compare alternative functional response within species for each of the data sets. For models 2 and 3, I used the same equations to fit mortality curves except that $Y = q$ (the catchability coefficient) and the right hand side of each of the models was divided by X . In the case of the type I mortality curve (model 1), I fit a simple linear regression with an intercept (i.e. $Y = a + bX$). The slope $b = 0$ (i.e. constant catchability) is

expected from a type I response.

Parameter Estimation

For both functional response curves and mortality curves, I fit model 1 by linear regression and models 2 and 3 by nonlinear least squares. Linear regressions were performed using the statistical package *Midas* (Fox and Guire 1976) and the technique is explained in detail in most statistical texts (e.g. Zar 1974). Nonlinear least squares is much less commonly applied by biologists and therefore, a few comments concerning nonlinear least squares techniques are warranted.

Nonlinear least squares methods require starting guesses of each parameter. Given these starting values, the methods use a variety of techniques to determine values that are used in subsequent iterations. The goal of any nonlinear least squares method is to find the parameter combinations that result in the so called *global minimum* SSE while avoiding convergence on slightly larger SSE (called *local minima*). For nonlinear least squares problems, the sums of squares surface can be quite irregular with several local minima. Thus, most nonlinear least squares fitting procedures are prone to false convergence on local minima, particularly if (1) initial guesses of starting parameters are poor, (2) only a narrow range of starting parameters are used in consecutive trial fits and (3) convergence criteria (i.e. the minimum acceptable difference between consecutive sets of parameter estimates) are too large (Vaessen 1984; Bates and Watts 1988).

To avoid these potential problems, I chose initial starting values of a equal to the maximum observed LPE for each data set and values of b and/or c

that resulted in a slope of the rising portion of the curve being roughly equivalent to the slope of a regression fit to the data (with an intercept). Since I had no independent estimates of parameters, I also compared the fit (i.e. the SSE) of each model fit to each data set with varying combinations of starting parameters. Thus, in addition to the initial set of starting values, I compared fits using double the initial parameter values, half the initial values and combinations with each individual parameter multiplied by 10 and 0.1 while holding the others constant. Thus for model 2, I used seven different starting parameter combinations and for model 3, I used nine different starting parameter combinations and these combinations covered a wide range of starting values for each of the models. I used 10^{-9} as my convergence criteria in all fits of the models. The parameter estimates that yielded the smallest SSE were considered the "best" fit estimates. All models were fit using a *Fortran* program that employed nonlinear fitting subroutines described in UBC NLP (Vaessen 1984). I used the routines FLETCH and FNMIN. Both routines employ a quasi-Newton search method, however FNMIN is less prone to false convergence (Vaessen 1984).

Comparison of Models

Note that each more complex model(s) (i.e. the model with more parameters) reduces to the simpler model(s) for certain parameter conditions. For example, model 2, the disc equation, reduces to model 1 when $1/b$ approaches zero (i.e. when b and a are large relative to X). Similarly, model 3 reduces to model 2 when $c = 0$ (and $1/a > 0$), and model 3 reduces to model 1 when $c=0$ and $1/b=0$ (i.e. as for model 2 above; for other parameter conditions where model 3 reduces to models 2 and 1 see Ch. 5). Thus models 1-3 can be

considered *nested* models; each simpler model is just a special case of the next most complex model.

Therefore, to compare these nested models (i.e. to determine the simplest model that adequately fits the data), I used the extra sums of squares test (Bates and Watts 1988). The test statistic is

$$[(SSE_p - SSE_f)/v_e]/[SSE_f/v_f] \quad (8.4)$$

where SSE_p is the residual sums of squares for the partial model (i.e. the model with fewer parameters), SSE_f is the residual sums of squares for the full model. v_e is the degrees of freedom for the sums of squares due to the extra parameter(s), and is equal to the difference in the numbers of parameters of the full (f) and partial (p) models (i.e. $P_f - P_p$). The degrees of freedom for the full model is $v_f = N - P_f$. The statistic is compared to $F(v_e, v_f, \alpha)$ and the extra parameter is retained if the calculated mean square ratio is greater than the table value (I used F tables in Zar 1974). I calculated the test statistics for three model comparisons: (1) model 1 vs. model 2, (2) model 1 vs. model 3, and (3) model 3 vs. model 2.

The null hypotheses for these comparisons were:

1. $H_o: 1/b=0$; i.e. a and $b \gg X$.
2. $H_o: c=0$ and $1/b=0$; i.e. a and $b \gg X$.
3. $H_o: c=0$.

I restricted my statistical comparisons to the functional response fits only because q estimates used for the mortality curves came directly from abundance estimates (e.g. abundance is in the denominator of eq. 7.14). Thus, an apparent inverse relationships between q and N (i.e. indicating a type II response) may

arise simply from random errors in abundance estimates (i.e. the X variate; Shardlow et al. 1985). My main purpose in fitting the q vs. abundance curves was to describe the shape of the relationships for each of the alternative models. Thus, I restricted my comparisons of mortality curves to qualitative comparisons of r^2 and residual mean squared errors (MSE). However, for the linear model I tested the null hypothesis that the slope, $b=0$ (using a 2-tailed t test), as would be expected from a type I functional response. I calculated the significance of each single species mortality model using equation 8.4 with SSE_p equal to the total sum of squared deviations from the mean q for each data set.

Calculation of Power

I calculated the statistical power (i.e. the probability of detecting an effect when it exists; Cohen 1977) for all cases where I failed to reject the null hypotheses in the extra sums of squares tests. The purpose of calculating power was that a failure to reject the above null hypotheses means that effect of the additional parameter is not significant and therefore the simpler model is as adequate as the more complex model in explaining the data. However, it is incorrect to assert that the simpler model is adequate (i.e. accept H_0), if the probability of making a type II error (i.e. β , the probability of failing to rejecting H_0 when it is false) is high. Power is simply $1-\beta$; thus when power is low there is a high probability of accepting H_0 when it is false. In contrast, α , which is normally set at 0.05, is the probability of rejecting the null hypothesis when it is true.

The power of any given test is a function of three factors: (1) the chosen α level, (2) the sample size (N), and (3) the effect size (ES). The effect size is

the true magnitude of the effect or "the degree to which the null hypothesis is false" (Cohen 1977). For example, the effect size in the test of the null hypothesis for model 1 vs. model 2 above, would be the degree to which the true $1/b$ is different from zero, or graphically the degree of nonlinearity in the functional response. If the data have come from an underlying functional response that is very nonlinear (i.e. saturating), then for a given sample size and α (i.e. 0.05) there will be a higher probability of rejecting H_0 (i.e. higher power), than if the true underlying response is less nonlinear. Similarly, because the critical values of a test statistic increase with decreasing N and increasing α , a large sample size will have a higher power than a smaller sample size, for a given α and ES, and a smaller α will result in lower power for a given N and ES.

Details of the calculations for power can be found in various statistical texts (e.g. Dixon and Massey 1969; Cohen 1977). In the case of F tests, procedures use the noncentral F distribution and therefore require the calculation of the noncentrality parameter (usually called λ ; not to be confused with the weighting factors for CAGEAN's auxiliary sums of squares, Ch. 7). For the power of the extra sums of squares F test, the noncentrality parameter measures how far the true curve (assumed to be the more complex model) is from the hypothesized curve (i.e the simpler model). In a graphical sense, the noncentrality parameter quantifies the degree to which the curve for the simple model fails to fit the curve the more complex model. The noncentrality parameter λ is estimated by the following formula:

$$\lambda = [\sum (Y_f - Y_p)^2 / v_e] / [SSE_f / v_f] \quad (8.5)$$

where Y_f are the predicted values from the full model using the best fit parameter estimates,

Y_p are the predicted values for the partial model when it is fit to the predicted values for the complex model and all other terms are as defined in equation 8.4 (R. Lockhart, Dept. of Statistics, Simon Fraser Univ., pers. comm.). $Y_f - Y_p$ is the deviation of the partial model from the full model at each observed value of the X variate (i.e. abundance). To estimate the sums of squares of these deviations, I fit each simpler model to the predicted values of the more complex models for each of the three comparisons above. Thus, for the comparisons of models 2 and 3 vs. model 1, I used simple linear regression through the origin (i.e. I fit model 1 to the predicted value from models 2 and 3). For the comparison of model 3 vs. model 2, I used nonlinear least squares to fit the model 2 to the predicted values of model 3. Given an estimate of λ , the test statistic, ϕ , used to estimate power is simply $\sqrt{[\lambda(v_e + 1)]}$, where v_e is the difference between the number of parameters in the full and partial models as define above. I used the power charts in Pearson and Hartley (1976) to determine the power given ϕ , the degrees of freedom, $v_1 = v_e$, $v_2 = v_f$, and $\alpha = 0.05$.

I also estimated the power for cases where I failed to reject the null hypothesis of zero slope in the linear mortality model. In this case, the noncentrality parameter, δ , is calculated by a nearly identical formula used for the t statistic. That is, $\delta = \text{ABS}(\beta - \beta_o) / \text{SE}_\beta$, where ABS denotes absolute value, $\beta_o = 0$, and SE_β is the standard error of the estimated slope (β). Given δ , $\text{df} = N - 2$, and the chosen significance level α , power can be determined using tables given in Dixon and Massey (1969). I used a **Fortran** program that calculated power exactly by linear interpolation for δ values that are between Dixon and Massey's tabulated values (R. Peterman, Simon Fraser Univ., pers. comm.).

Examination of Residuals

Statistical tests for linear and nonlinear least squares methods assume normality and homoskedasticity of residuals. Violations of either or both of these two assumptions may result in biased parameter estimates and/or biased test statistics, although the F test is reportedly robust to deviations from normality (Zar 1974, Neter and Wasserman 1974). Extreme deviations from normality and homoskedasticity suggest that the fitted model is inappropriate for the data.

I tested the residuals from fits of each model for normality using the Anderson-Darling test statistic, A^2 , as modified by Stephens (1974). Monte Carlo trials have shown that the modified A^2 statistic provides a more powerful test of normality than the Kolmogorov-Smirnov statistic and others (Stephens 1974). The null hypothesis for the test is that the residuals came from a normal distribution. I used a **Fortran** program to calculate the modified A^2 values (Paul Higgins, Natural Res. Mgt. Prog., Simon Fraser Univ., pers. comm.) and compared the calculated values to the critical values in the table in Stephens (1974; Case 3) with N-P degrees of freedom.

To assess the homoskedasticity of the residuals, I calculated rank correlations (Kendall's τ_b ; Seigel 1956) between the absolute values of the residuals and the values of the X variates (Neter and Wasserman 1974; Peterman 1981). The null hypothesis is that there is no association between the absolute value of residuals and the X variate (i.e. abundance). I calculated τ_b values and their significance using **Midas** (Fox and Guire 1976).

Multispecies Models

I fit the multispecies disc equation (MSDE; Murdoch 1973) below to data for all three species in an attempt to model the whole system as a unit.

$$Y = aX/[1 + bX + cX_1 + dX_2] \quad (8.6)$$

where Y is LPE (i.e. NA/T_p), X is abundance the species being consider in Y , X_i is the abundance of alternative prey i , and a , b , c and d are parameters to be estimated.

The general pattern of landings and effort suggests that usually cod and English sole are caught together in somewhat deeper waters (30-49 vs. 10-19 fathoms) than rock sole (Westrheim and Foucher 1985a). Thus, the most logical structure for a MSDE would consider cod and English sole (i.e. X_i s in as the alternatives to rock sole. However, the pattern of landings for the three species varied seasonally and among years (see Section on 'Study area and fishery description' in Ch. 7), and this variability warranted fitting the model to the other species as well.

Thus, for cod, the X_i s were the abundances of English sole and rock sole, and similarly for English sole, X_i s were rock sole abundance and cod abundance. For each species, I used catch and abundance estimates from the same two age ranges and methods used for the analysis of single species responses. Thus I used 4 data sets for each species.

I fit equation 8.6 to each of these data sets using nonlinear least squares. In order to obtain some reasonable estimate of initial starting

parameters for each data set, I fit the linearized version of equation 8.6 shown below.

$$1/Y = b/a + 1/(aX) + cX_1/(aX) + dX_2/(aX) \quad (8.7)$$

where all variables and parameters are the same as in equation 8.6. I fit equation 8.7 by multiple linear regression and used the resulting regression coefficients (i.e. b/a , $1/a$, and c/a , and d/a) to solve for the initial starting values of a , b , c and d . I took the same precautions described above for the single species models to avoid false convergence on local minima.

I also fit the linear model below (by multiple linear regression) for comparison with the MSDE.

$$Y = a + bX + cX_1 + dX_2 \quad (8.8)$$

Note that when the parameters c , and d of the linear and MSDE equations have opposite signs, the two models predict the same qualitative effects of alternative prey abundances on LPE. I restricted my comparison of the linear model (i.e. eq. 8.8) and the MSDE to r^2 values, because the models were not nested (i.e. each had the same number of parameters), and therefore, the extra sums of squares test was not appropriate (it would have zero degrees of freedom). Similarly, because the data sets for both multispecies models included only the period of overlap in the data sets for each species (i.e. 1961-78 for cod, English sole and rock sole), I was unable to compare the fits of the multispecies and singles species models. However, a sizeable difference in the r^2 s between the best fit single and multispecies model for given data set would at least provide weak evidence as to which approach was best. In addition, I also

tested the residuals from fitting each multispecies model for normality by the methods described above.

I used equations similar to 8.6 and 8.8 to fit the mortality curves for the multispecies models. For the linear model, I used an equation identical to 8.8, except that $Y = q$. For the MDSE, I used equation 8.6 with $Y = q$, and where the right hand side was divided by X as in the single species models. I fit these two models by multiple linear regression and nonlinear least squares, respectively. Again, I restricted my comparison between the multispecies models to r^2 values, and my main purpose was to describe the shape of the functional relationship between q and abundance in a multispecies system. As with the functional response, I limited my comparisons of single and multispecies mortality curves to the r^2 values.

Tests of the Switching Hypothesis

I used the model below to test the switching null hypothesis (cf. with eq. 5.16, Ch. 5):

$$C_1/C_2 = a(N_1/N_2)^\beta \quad (8.9)$$

where C and N are the landed catches per unit effort and abundances for species 1 and 2, and a and, β are parameters to be estimated. A value of $\beta > 1.0$ indicates that the ratio of C 's is increasing faster than linearly as the ratio of abundances increases, and switching is indicated. I estimated a and, β using the log transformed version of equation 8.9 shown below.

$$\ln(C_1/C_2) = \ln(a) + \beta \ln(N_1/N_2) \quad (8.10)$$

I fit equation 8.10 by linear regression and tested the null hypothesis of

$H_0: \beta \leq 1.0$ using a one-tailed t -test (Zar 1974).

For cases where I failed to reject H_0 , I estimated the power using the noncentrality parameter δ as described above only with $\beta_0 = 1.0$. In addition to calculating power, I also tested the residuals from fits of equation 8.10 for normality and homoskedasticity by the same tests used for the functional response models (see above).

Data for the same age ranges and two methods were used in the tests of the switching hypothesis as for the previous analyses. I expect evidence for switching to be the strongest between cod and rock sole because these two species are generally caught at different depths, and therefore fishermen can easily target on either species while excluding the other. However, I tested the switching hypothesis for all 12 data sets (3 species pairs \times 2 age ranges \times 2 catch-at-age methods).

Results

Comparison of Single Species Functional Response Models

Pacific cod

All three alternative functional response models fit each of the cod data sets reasonably well (all r^2 s ≥ 0.68 ; Table 8.1). Best fit parameter values for models 1 (linear) and 2 (disc) resulted in identical curves for all data sets; thus, the best fit disc equation was linear (Fig. 8.1). The best fit parameters for Fujii et al.'s (1978) generalized equation (model 3) were consistent with a type III (sigmoid) response for all data sets, although the curve for one data set reaches an asymptote at about double the observed maximum in abundance (VPA ages

Pacific cod

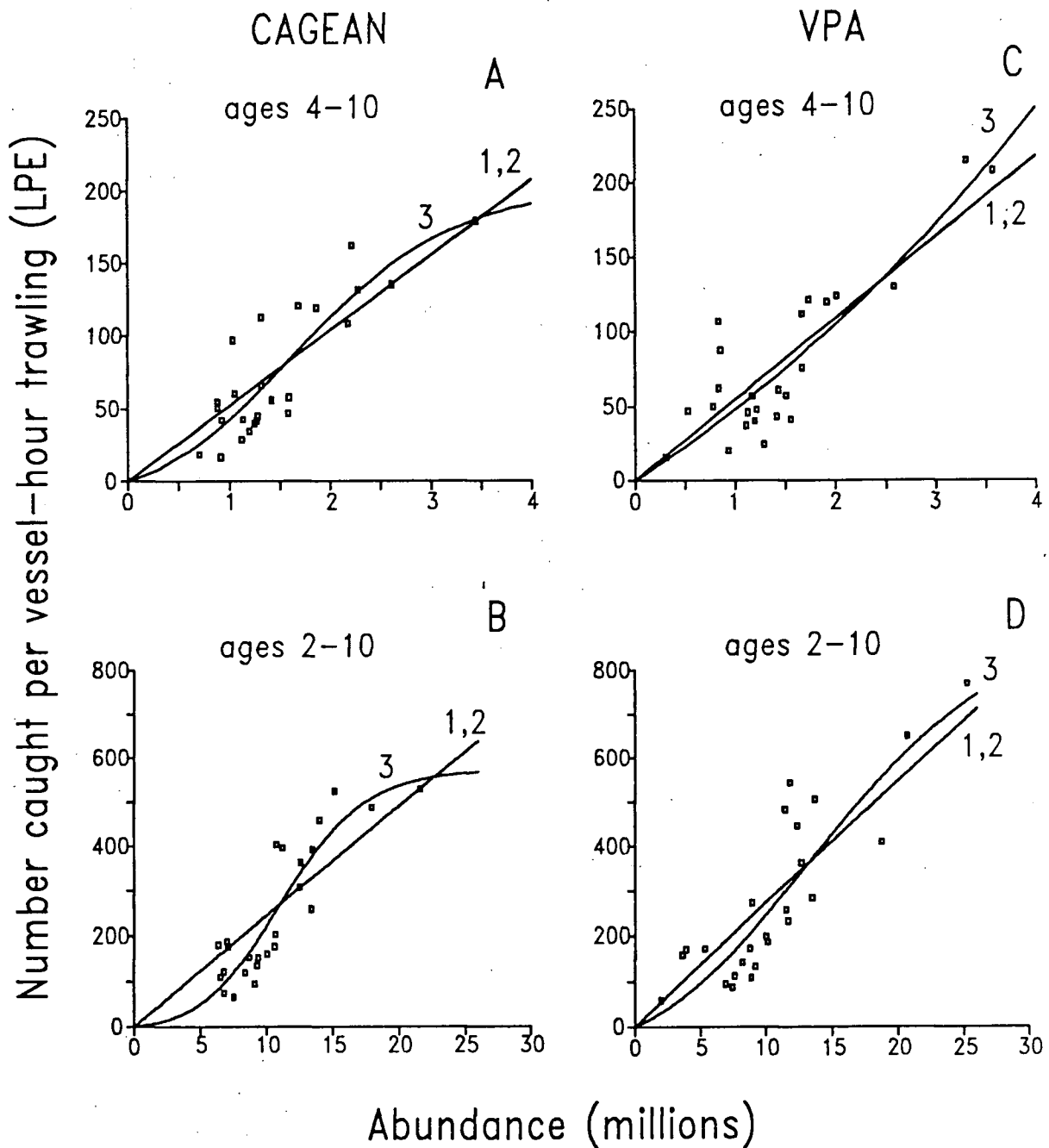


Figure 8.1. Comparison of alternative single species functional response model fits to Pacific cod data sets. Squares are observations and predicted lines were drawn using the best fit parameters (Table 8.1). Numbers beside lines denote the model number; 1=linear, 2=disc, 3=generalized equation. Panels A and B use data sets from CAGEAN for ages 4-10 and 2-10 and panels C and D use data sets from VPA for the same age ranges. Note: lines for models 1 and 2 were coincident for all data sets.

4-10; Fig. 8.1 C).

Extra sums of squares tests were not performed for model 1 vs. model 2 comparisons because model 2 had slightly larger SSE than model 1 for all data sets (Table 8.1). Model 3 consistently had the smallest MSE and largest r^2 s (Table 8.1). However, the only significant differences among curves were for the data set from CAGEAN ages 2-10 where model 3 had significantly improvement in fit compared to either model 1 or 2 (Table 8.1).

Where the null hypothesis for the extra sums of squares test was not rejected, power was low (<0.35 ; Table 8.1). Thus, for these cases, it would be incorrect to conclude that the simpler model was sufficient because of the large probability (>0.65) of making a type II error.

Residuals from fits of models 1 and 2 were generally positive at high abundance and negative at low abundance with the exception of the data set from VPA ages 4-10 (Fig. 8.1). There was no evidence for heteroskedasticity in the residuals from any of the model-data set combinations as all τ_b were not statistically significant (Table 8.1). The null hypothesis of normality was rejected for 3 out of 4 data sets for models 1 and 2, but for only 1 data set fit by model 3 (CAGEAN ages 4-10). Thus, the model 3 fits were most consistent with the assumptions of least square methods.

Models fit to data from the two catch-at-age methods had similar curves. However, fits of models 1 and 2 had consistently steeper slopes and fits of model 3 had consistently larger asymptotes for VPA data sets than for CAGEAN data sets (Fig. 8.2).

Table 8.1. Summary statistics for single species functional response model comparisons for Pacific cod. For left to right are the data source (age range and method), model number ($Y=\bar{Y}$ denotes fitting data with mean \bar{Y} , 1=linear, 2=disc, 3=generalized equation), the parameter values a , b , and c as appropriate, the residual sums of squares (SSE), the coefficient of determination (r^2), the degrees of freedom (df, $n=25$), the residual mean square error (MSE), the F statistics for the extra sums of squares test (top 1 vs. 2, middle 1 vs. 3, bottom 2 vs. 3), and corresponding P values (— indicates F statistic and P value not computed because $SSE_f > SSE_p$, see text). For those cases where the F was not significant at $P < 0.05$, the noncentrality parameter, phi, and the power of the F test are also given. Statistics for tests of residuals include for the normality test, Stephens' (1974) modified A^2 statistic and corresponding P value, and for the homoskedasticity test, Kendall's τ_b and corresponding P value.

Data source	Model	Parameters			SSE	r^2	df	MSE	F	P	phi	Power	Normality	Homoskedasticity	
		a	b	c									Modified A^2	P τ_b	P
Ages 4-10 CAG	$Y=\bar{Y}$				50829		24	2118	—	—	—	—			
	1	0.0518			15141	0.70	24	631	—	—	—	—	0.78	<0.05 -0.06	>0.69
	2	3.40E+6	6.55E+7		15145	0.70	23	658	1.34	>0.25	0.68	<0.15	0.78	<0.05 -0.06	>0.69
	3	205	9043	-8.50E-4	13499	0.73	22	614	2.68	>0.10	1.18	<0.35	0.83	<0.025 -0.07	>0.63
	$Y=\bar{Y}$				67075		24	2795							
	1	0.0544			18201	0.73	24	758	—	—	—	—	0.36	>0.15 -0.05	>0.73
	2	1.37E+7	2.51E+8		18202	0.73	23	791	1.04	>0.25	0.59	<0.15	0.36	>0.15 -0.05	>0.73
	3	115807	2.65E+6	-9.40E-5	16632	0.75	22	756	2.08	>0.10	1.02	<0.25	0.51	>0.15 -0.07	>0.63
	$Y=\bar{Y}$				537040		24	22377							
	1	0.0245			172570	0.68	24	7190	—	—	—	—	0.79	<0.05 0.13	>0.63
	2	2.26E+6	9.21E+7		172587	0.68	23	7504	5.76	<0.01	n/a	n/a	0.79	<0.05 0.07	>0.63
	3	574	174342	-2.40E-4	113241	0.79	22	5147	11.53	<0.005	n/a	n/a	0.48	>0.15 -0.03	>0.84
Ages 2-10 VPA	$Y=\bar{Y}$				871680		24	36320							
	1	0.0274			244230	0.72	24	10176	—	—	—	—	1.12	<0.01 0.20	>0.17
	2	2.38E+6	8.69E+7		244296	0.72	23	10622	1.12	>0.25	0.63	<0.15	1.04	<0.01 0.20	>0.17
	3	933	68691	-9.23E-5	221602	0.75	22	10073	2.25	>0.10	1.10	<0.30	0.65	>0.05 0.07	>0.63

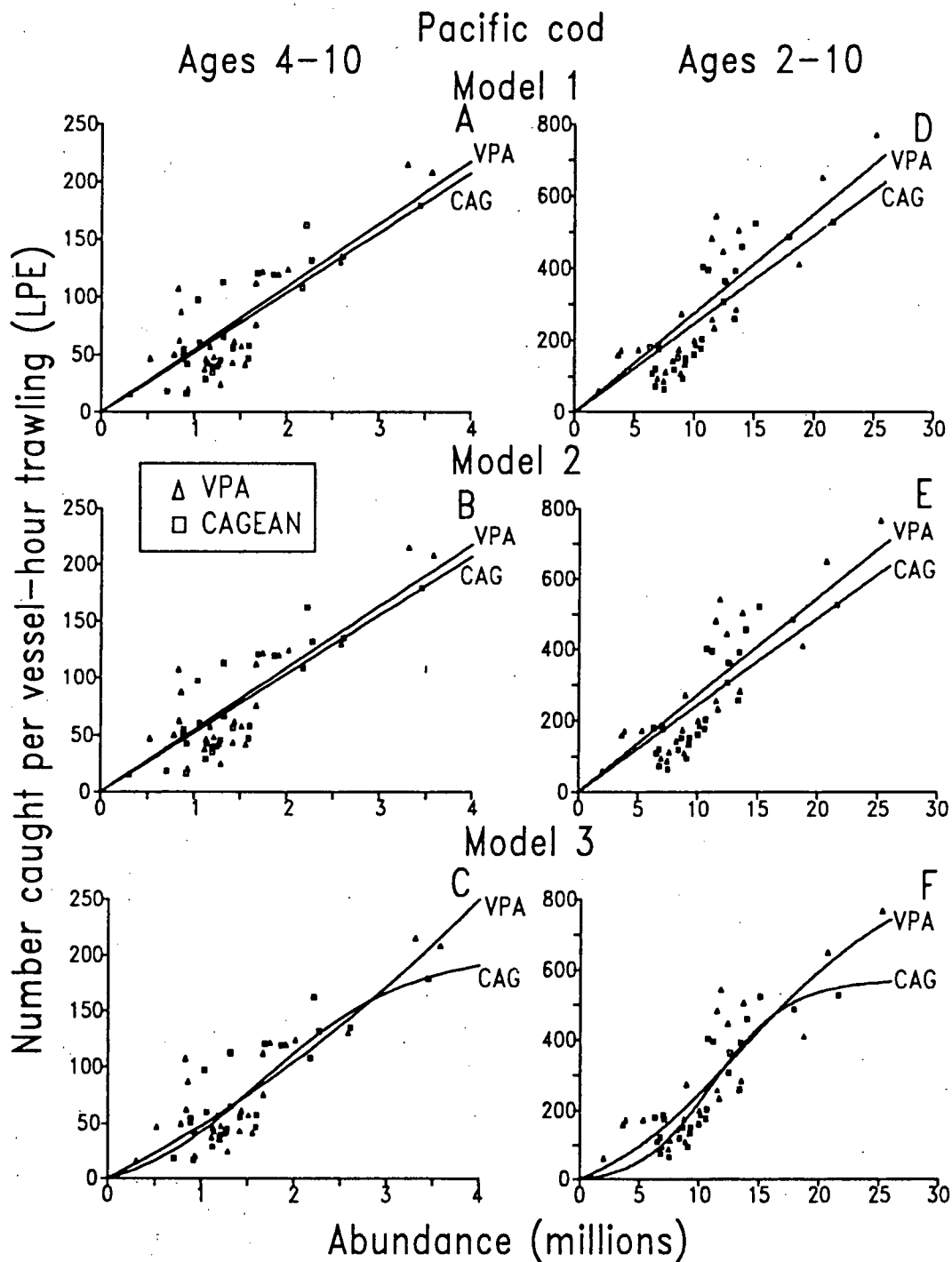


Figure 8.2. Comparison of alternative single species functional response models from VPA and CAGEAN fit to data sets for Pacific cod. Squares and triangles are observations from CAGEAN and VPA. Predicted lines are drawn using the best fit parameters (Table 8.1). Labels beside lines (VPA and CAG) denote catch-at-age methods. Model numbers are indicated above each pair of horizontal panels. Panels A, B and C use data sets for ages 4-10 and panels D, E and F use data sets for ages 2-10.

English sole

All of the alternative models fit the data sets for English sole poorly, although fits to the data sets for fully recruited ages (6-10) were somewhat better ($0.21 \leq r^2 \leq 0.37$) than fits to data sets for all ages (3-17; $0.02 \leq r^2 \leq 0.12$; Table 8.2). In contrast with the fits to cod data sets, all fits of model 2 were nonlinear and consistent with a type II response (Fig. 8.3). Parameter values for model 3 were consistent with a type III response for 3 out of 4 data sets (exception was CAGEAN ages 3-17; Fig. 8.3 B).

However, none of these qualitative differences was statistically significant; the null hypothesis for the extra sums of squares test was not rejected for any of the model comparisons (Table 8.2). While model 1 had the smallest MSE for each data set, power was low (<0.15) for all model comparisons. Therefore, as for cod, it is incorrect to conclude that the simpler models were sufficient because of the high probability (>0.85) of a type II error (Table 8.2).

Residuals from all models were not significantly heteroskedastic by the rank correlation test (Table 8.2). However, the distributions of residuals were significantly nonnormal for all model fits ($P < 0.01$; Table 8.2).

Data sets from VPA and CAGEAN resulted in similar curves, except that the model 3 fit to data from ages 3-17 was sigmoid for VPA and saturating for CAGEAN (Fig. 8.4 F).

Table 8.2. Summary statistics for single species functional response model comparisons for English sole. From left to right are the data source (age range and method), model number (Y=Y denotes fitting data with mean Y, 1=linear, 2=disc, 3=generalized equation), the parameter values a , b , and c as appropriate, the residual sums of squares (SSE), the coefficient of determination (r^2), the degrees of freedom (df; $n=23$), the residual mean square error (MSE), the F statistics for the extra sums of squares test (top 1 vs. 2, middle 1 vs. 3, bottom 2 vs. 3), and corresponding P values (— indicates F statistic and P value not computed because $SSE_f > SSE_p$, see text). For those cases where the F was not significant at $P < 0.05$, the noncentrality parameter, phi, and the power of the F test are also given. Statistics for tests of residuals include for the normality test, Stephens' (1974) modified A^2 statistic and corresponding P value, and for the homoskedasticity test, Kendall's τ_b and corresponding P value.

Data		Parameters											Normality	Homoskedasticity		
source	Model	a	b	c	SSE	r ²	df	MSE	F	P	phi	Power	Modified A ²	P	tau _b	P
Ages	Y=Ȳ				390070		23	16960								
6-10	1	0.1380			308450	0.21	23	13411	0.37	>0.25	0.37	<0.10	1.91	<0.01	0.00	>0.98
CAG	2	947.62	5221.42		303331	0.22	22	13788	0.54	>0.25	0.29	<0.10	1.80	<0.01	-0.11	>0.48
	3	279	6508	-1.96E-3	293427	0.25	21	13973	0.71	>0.25	0.44	<0.10	2.10	<0.01	0.03	>0.88
Ages	Y=Ȳ				483890		23	21039								
6-10	1	0.1370			368810	0.24	23	16035	0.80	>0.25	0.55	<0.15	2.12	<0.01	0.12	>0.42
VPA	2	862	4443		355908	0.26	22	16178	2.21	>0.10	0.41	<0.10	2.03	<0.01	-0.10	>0.51
	3	310	3678	-1.17E-3	304713	0.37	21	14510	3.53	>0.05	0.52	<0.15	2.00	<0.01	0.03	>0.86
Ages	Y=Ȳ				1398100		23	60787								
3-17	1	0.0588			1402400	—	23	60974	0.51	>0.25	0.56	<0.15	1.45	<0.01	-0.06	>0.71
CAG	2	705	5410		1370808	0.02	22	62309	0.24	>0.25	0.32	<0.10	1.24	<0.01	-0.12	>0.42
	3	705	5410	1.06E-10	1370808	0.02	21	65277	—	—	—	—	1.24	<0.01	-0.12	>0.42
Ages	Y=Ȳ				2098200		23	91226								
3-17	1	0.0673			1893400	0.10	23	82322	0.22	>0.25	0.29	<0.10	1.82	<0.01	0.14	>0.36
VPA	2	1583	16812		1874338	0.11	22	85197	0.27	>0.25	0.25	<0.10	1.87	<0.01	0.04	>0.79
	3	520	39276	-5.95E-4	1845755	0.12	21	87893	0.33	>0.25	0.34	<0.10	1.78	<0.01	0.12	>0.45

English sole

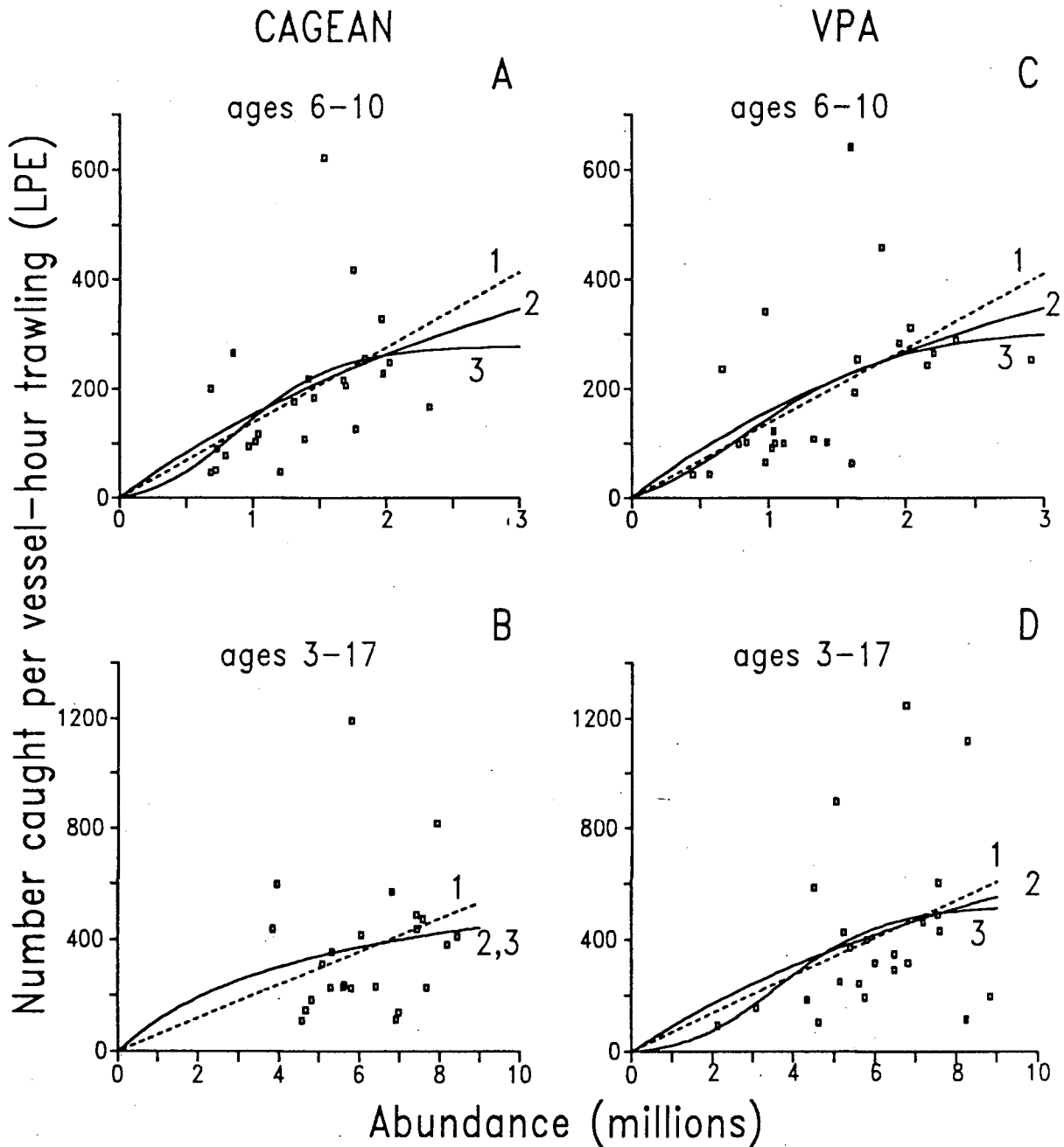


Figure 8.3. Comparison of alternative single species functional response model fits to English sole data sets. Squares are observations and predicted lines were drawn using the best fit parameters (Table 8.2). Numbers beside lines denote the model number; 1=linear, 2=disc, 3=generalized equation. Dotted line is for model 1. Panels A and B use data sets from CAGEAN for ages 6-10 and 3-17 and panels C and D use data sets from VPA for the same age ranges.

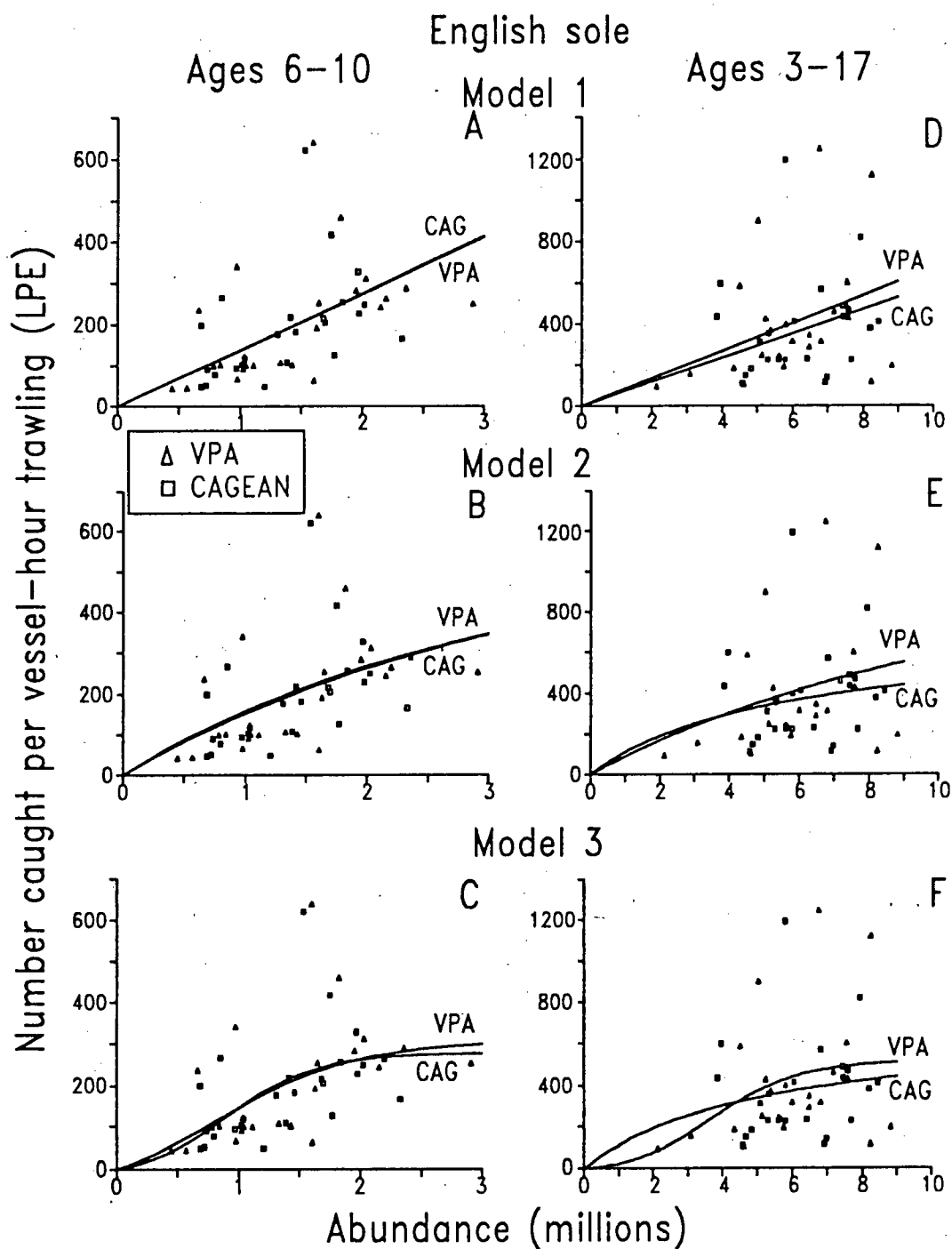


Figure 8.4. Comparison of alternative single species functional response models from VPA and CAGEAN fit to data sets for English sole. Squares and triangles are observations from CAGEAN and VPA. Predicted lines are drawn using the best fit parameters (Table 8.2). Labels beside lines (VPA and CAG) denote catch-at-age methods. Model numbers are indicated above each pair of horizontal panels. Panels A , B and C use data sets for ages 6-10 and panels D, E and F use data sets for ages 3-17.

Rock sole

The fits of alternative functional response models to the rock sole data sets had intermediate r^2 values compared to the fits for the cod and English sole data sets. As found for English sole, r^2 values were higher for all models when fit to data for fully recruited ages (6-10; $0.33 \leq r^2 \leq 0.56$), than when fit to data for all ages (3-17; $0.21 \leq r^2 \leq 0.34$; Table 8.3).

Best fit parameters for models 1 and 2 resulted in nearly identical curves for all data sets. Thus as found for cod, model 2 fits were linear (Fig. 8.5). Model 3 fits to all data sets resulted in sigmoid curves, although the asymptote for one data set (VPA ages 6-10) occurred outside the range of observed abundances (at about 4000; Fig. 8.5 C).

Model 3 had the smallest MSE for 3 out of 4 data sets, and three model comparisons found significant differences (model 2 vs. 3 for CAGEAN ages 6-10 and models 1 and 2 vs. 3 for VPA ages 6-10 ;Table 8.3). Power was generally low, although somewhat higher for model 2 vs. 3 comparisons (min. power<0.35; max. power<0.40) than for the two other model comparisons (min. power<0.05; max. power<0.30; Table 8.3). Thus for all cases where the extra sums of squares test was not rejected, it is incorrect to conclude that the simpler models were sufficient.

Data sets for rock sole were the only ones where I found significant heteroskedasticity in residuals by the rank correlation test. Residuals were significantly heteroskedastic for the fits of models 1 and 2 to VPA data sets for ages 6-10, and for all model fits to VPA data sets for ages 4-15 (Table 8.3).

Table 8.3. Summary statistics for single species functional response model comparisons for rock sole. From left to right are the data source (age range and method), model number ($Y=\bar{Y}$ denotes fitting data with mean Y , 1=linear, 2=disc, 3=generalized equation), the parameter values a , b , and c as appropriate, the residual sums of squares (SSE), the coefficient of determination (r^2), the degrees of freedom (df; $n=23$), the residual mean square error (MSE), the F statistics for the extra sums of squares test (top 1 vs. 2, middle 1 vs. 3, bottom 2 vs. 3), and corresponding P values (— indicates F statistic and P value not computed because $SSE_f > SSE_p$, see text). For those cases where the F was not significant at $P < 0.05$, the noncentrality parameter, ϕ , and the power of the F test are also given. Statistics for tests of residuals include for the normality test, Stephens' (1974) modified A^2 statistic and corresponding P value, and for the homoskedasticity test, Kendall's τ_b and corresponding P value.

Data		Parameters			SSE	r^2	df	MSE	F	P	phi	Power	Normality		Homoskedasticity	
source	Model	a	b	c									Modified A^2	P	τ_b	P
Ages	$Y=\bar{Y}$				1390800		22	63218	—	—	—	—	2.62	<0.01	-0.10	>0.53
6-10	1	0.2160			769600	0.45	22	34982	—	—	—	—	2.62	<0.01	-0.10	>0.53
CAG	2	3.01E+6	1.40E+7		769634	0.45	21	36649	2.51	>0.10	0.91	<0.30	2.62	<0.01	-0.10	>0.53
	3	897	44387	-1.65E-3	615120	0.56	20	30756	5.02	<0.05	n/a	n/a	1.72	<0.01	0.26	>0.08
Ages	$Y=\bar{Y}$				5290500		22	240477					2.59	<0.01	0.32	<0.03
6-10	1	0.2780			3569200	0.33	22	162236	—	—	—	—	2.59	<0.01	0.32	<0.03
VPA	2	1.43E+7	5.13E+7		3569346	0.33	21	169969	3.75	<0.05	n/a	n/a	2.59	<0.01	0.32	<0.03
	3	2128	267564	-1.82E-3	2596418	0.51	20	129821	7.49	<0.025	n/a	n/a	1.77	<0.01	0.26	>0.09
Ages	$Y=\bar{Y}$				2814000		22	127909					1.20	<0.01	0.21	>0.17
4-15	1	0.1040			2216700	0.21	22	100759	0.03	>0.25	0.11	<0.05	1.20	<0.01	0.21	>0.17
CAG	2	6824	60711		2213325	0.21	21	105396	0.91	>0.25	0.57	<0.15	1.23	<0.01	0.18	>0.25
	3	628	367251	-1.46E-3	2031069	0.28	20	101553	1.79	>0.10	0.99	<0.35	0.64	>0.05	0.30	<0.05
Ages	$Y=\bar{Y}$				7214500		22	327932					2.07	<0.01	0.40	<0.007
4-15	1	0.1280			5711700	0.21	22	259623	0.06	>0.25	0.14	<0.05	2.07	<0.01	0.40	<0.007
VPA	2	5832	39720		5694728	0.21	21	271178	1.92	>0.10	0.77	<0.15	2.24	<0.01	0.34	<0.03
	3	871	2.93E+7	-2.48E-3	4793049	0.34	20	239652	3.76	>0.05	1.33	<0.40	1.09	<0.01	0.35	<0.02

rock sole

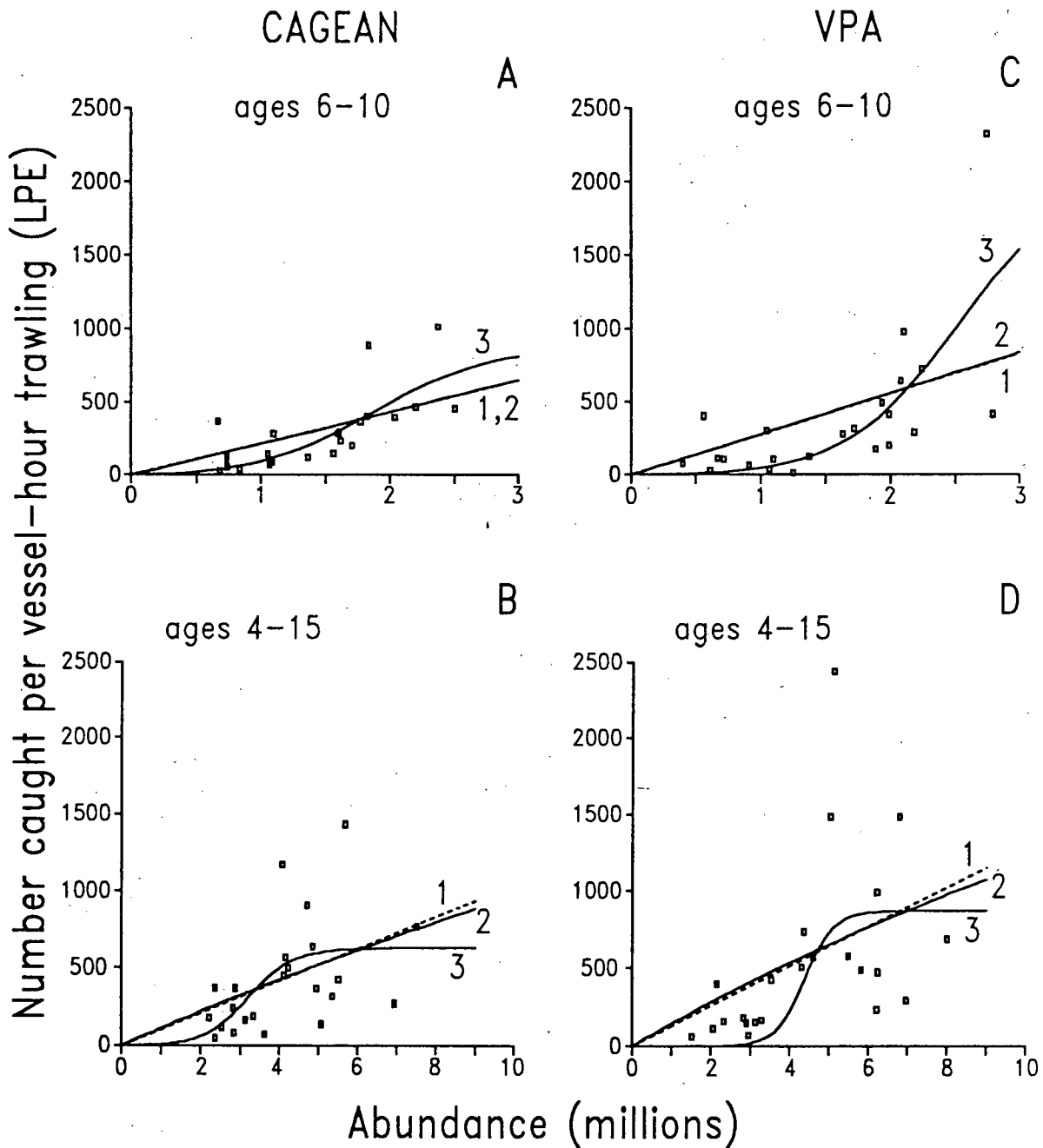


Figure 8.5. Comparison of alternative single species functional response model fits to rock sole data sets. Squares are observations and predicted lines were drawn using the best fit parameters (Table 8.3). Numbers beside lines denote the model number; 1=linear, 2=disc, 3=generalized equation. Dotted line is for model 1. Panels A and B use data sets from CAGEAN for ages 6-10 and 4-15 and panels C and D use data sets from VPA for the same age ranges.

However, residuals were significantly heteroskedastic for only one model-data set combination from CAGEAN (model 3 fit to ages 4-15; Table 8.3). Residuals from all model fits were highly significantly nonnormal ($P < 0.01$), with the exception of model 3 fit to the CAGEAN data set for ages 4-15 (Table 8.3).

Curves for each model fit to data sets from VPA and CAGEAN were similar. However, as found for the cod data sets, curves for models 1 and 2 had steeper slopes and curves for model 3 had larger asymptotes when fit to VPA data sets compared with fits to CAGEAN data sets (Fig. 8.6).

Single Species Mortality Curves

Pacific cod

All three mortality models fit the cod data sets poorly (all $r^2 \leq 0.24$; Table 8.4). Only the fits of the linear and Fujii models to the data set from CAGEAN for all ages (2-10) were statistically significant (Table 8.4). The slope of the fit of the linear model was significantly different from zero for only 1 data set (CAGEAN ages 2-10), where the slope was positive indicating an increase in q with abundance (Table 8.4). Power was low (≤ 0.29) for the other three data sets, indicating it would be incorrect to assert that q is density independent.

All fits of model 2 were equivalent to fitting a model of $q = \text{constant}$. Data sets from VPA resulted in larger intercepts (i.e. higher avg. q ; Fig. 8.8 B and E; Table 8.4). Model 3 fits to CAGEAN data sets were dome shaped, which is consistent with a sigmoid functional response (Fig. 8.7). Model 3 fits to VPA data sets were linear with zero slope for ages 2-10 and linear with a slightly decreasing slope for ages 4-10 (Figs. 8.7, 8.8). Thus, mortality relationships

Table 8.4. Summary statistics for single species mortality model fits to Pacific cod data sets. From left to right are the data source (age range and method), model number ($Y=\bar{Y}$ denotes fitting data with mean Y , 1=linear, 2=disc, 3=generalized equation), the parameter values a , b , and c as appropriate, the P values for the test of $H_0: b=0$ for the linear model, the power for the same test, the residual sums of squares (SSE), the coefficient of determination (r^2), the degrees of freedom (df; $n=25$ for CAGEAN and 24 for VPA), the residual mean square error (MSE), the F value for test of the significance of the fit, and the P value. Note: — indicates F and P value not computed because SSE of model was greater than or equal to SSE of $Y=\bar{Y}$.

Data source	Model	Parameters			$P(b b=0)$	Power	SSE	r^2	df	MSE	F	P
		a	b	c								
Ages	$Y=\bar{Y}$						2.35		24	0.10		
4-10	1	0.61	1.44E-4		0.15	0.29	2.14	0.09	23	0.09	2.18	0.15
CAG	2	5.19E+8	6.30E+8				2.35	—	23	0.10	—	—
	3	4042	9348	-7.20E-4			2.08	0.11	22	0.09	1.39	0.27
Ages	$Y=\bar{Y}$						4.92		23	0.21		
4-10	1	1.09	-7.98E-5		0.55	0.08	4.84	0.02	22	0.22	0.38	0.54
VPA	2	2.31E+8	2.39E+8				4.92	0.00	22	0.22	—	—
	3	240273	204075	1.31E-4			4.80	0.03	21	0.23	0.55	0.59
Ages	$Y=\bar{Y}$						0.41		24	0.02		
2-10	1	0.20	1.42E-5		0.04	—	0.34	0.17	23	0.01	4.69	0.04
CAG	2	3.19E+7	9.14E+7				0.41	—	23	0.02	—	—
	3	10286	101582	-1.67E-4			0.31	0.24	22	0.01	6.78	0.01
Ages	$Y=\bar{Y}$						0.72		23	0.03		
2-10	1	0.40	2.13E-7		0.98	0.03	0.72	0.00	22	0.03	0.00	1.00
VPA	2	3.53E+8	8.69E+8				0.72	0.00	22	0.03	0.00	1.00
	3	3.61E+6	8.94E+6	-7.01E-7			0.72	0.00	21	0.03	0.00	1.00

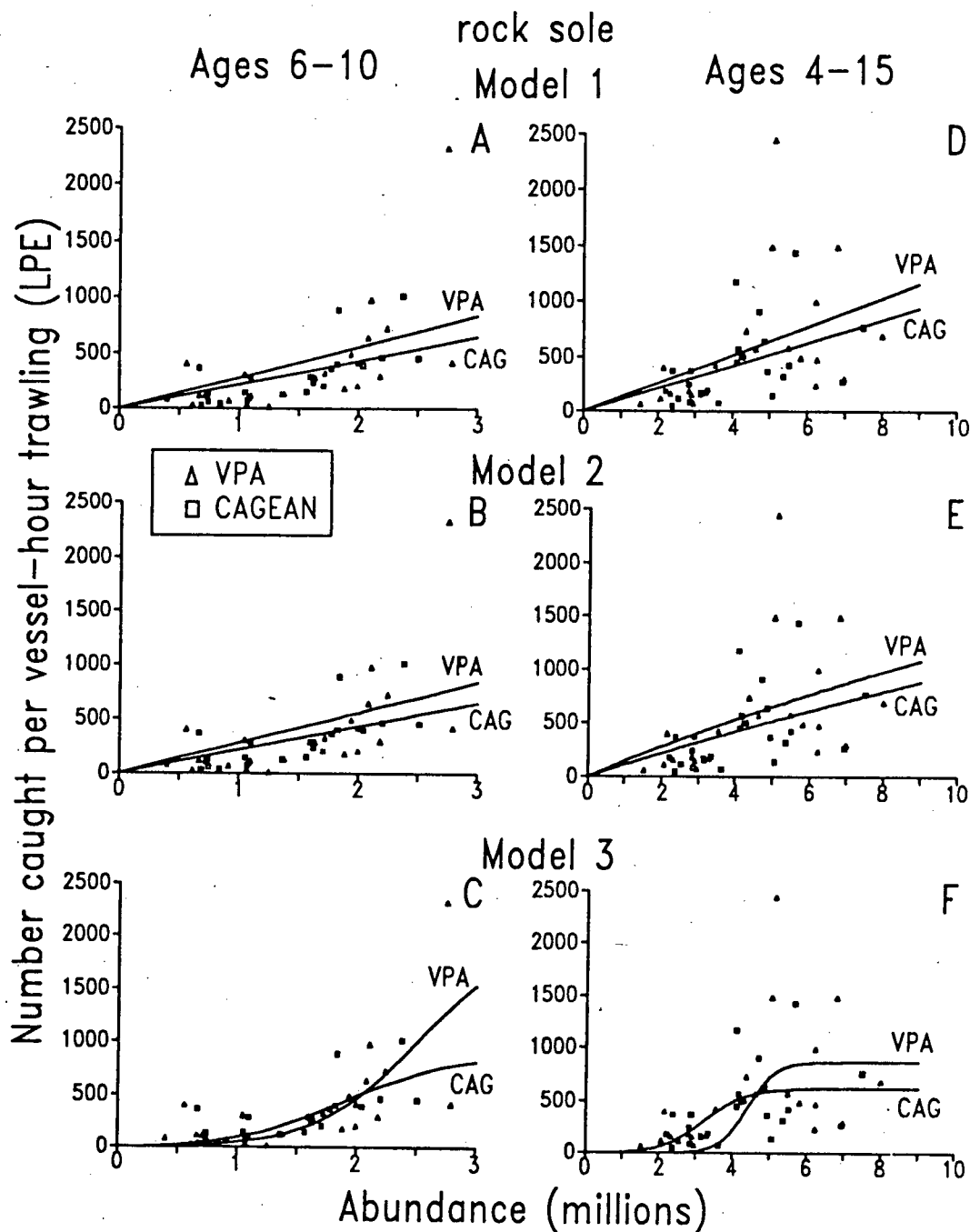


Figure 8.6. Comparison of alternative single species functional response models from VPA and CAGEAN fit to data sets for rock sole. Squares and triangles are observations from CAGEAN and VPA. Predicted lines are drawn using the best fit parameters (Table 8.3). Labels beside lines (VPA and CAG) denote catch-at-age methods. Model numbers are indicated above each pair of horizontal panels. Panels A, B and C use data sets for ages 6-10 and panels D, E and F use data sets for ages 4-15.

Pacific cod

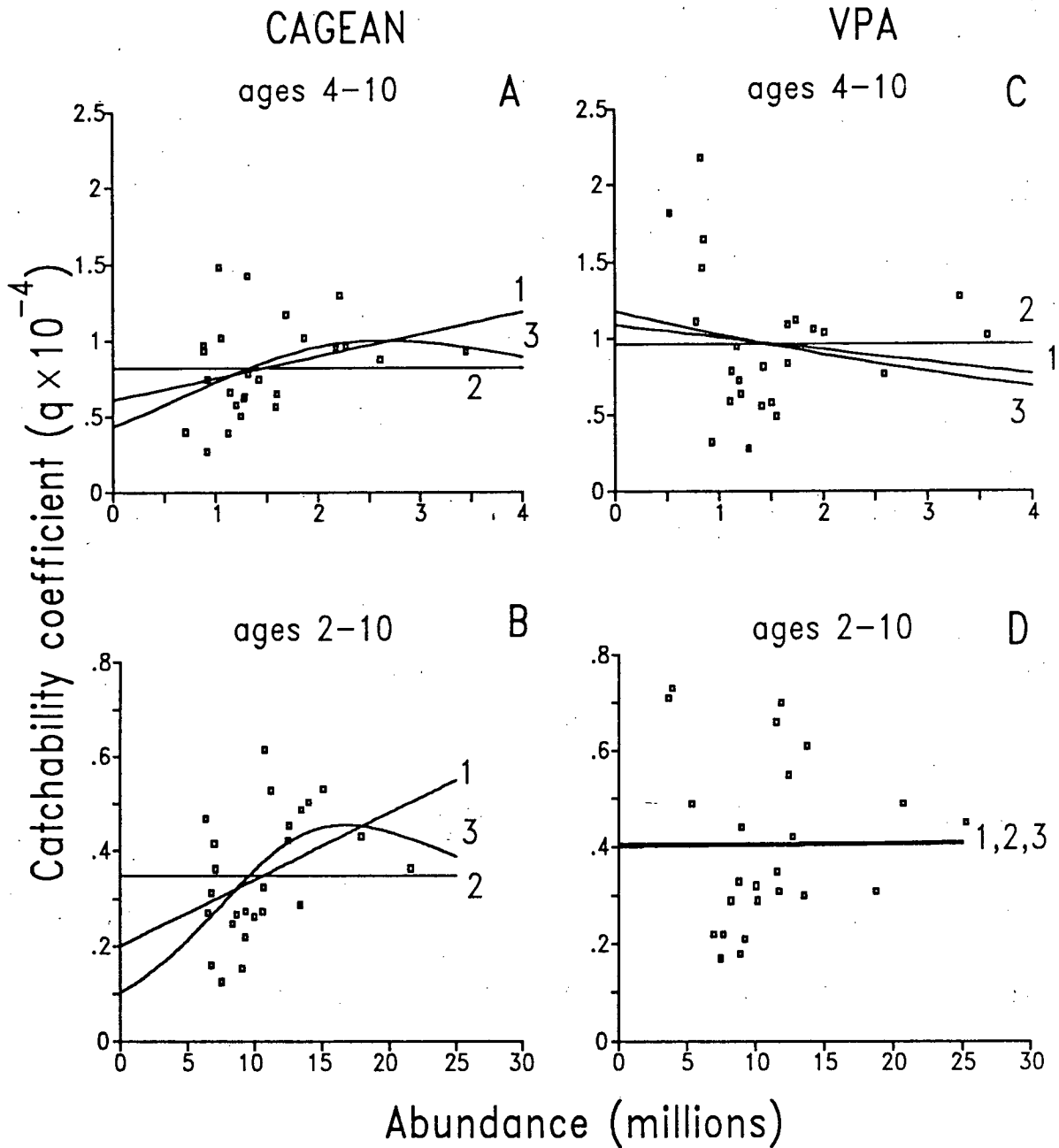


Figure 8.7. Comparison of alternative single species mortality model fits to Pacific cod data sets. Squares are observations and predicted lines were drawn using the best fit parameters (Table 8.4). Numbers beside lines denote the model number; 1=linear, 2=disc, 3=generalized equation. Panels A and B use data sets from CAGEAN for ages 4-10 and 2-10 and panels C and D use data sets from VPA for the same age ranges.

suggested by the best fit parameter estimates differed between VPA and CAGEAN data sets for models 1 and 3, but were virtually identical for model 2 (Fig. 8.8).

Mortality relationships were qualitatively consistent with functional responses for each model and data set, except that the mortality curve for model 3 and the VPA data set was linear whereas the functional response was slightly sigmoid. (cf. Figs. 8.2 and 8.8).

English sole

All three mortality models fit the English sole data sets poorly as none were significantly better than fitting the data with the average q for each data set (all r^2 s ≤ 0.07 , $P \geq 0.22$; Table 8.5). The null hypothesis of $b = 0$ for the linear model was not rejected for any of the data sets, although the power was consistently very low (≤ 0.17 ; Table 8.5). Thus, again it would be incorrect to conclude that q is density independent.

The predicted mortality relationships varied among models within each data set and among data sets for each model, with the exception that model 2 was nearly linear with decreasing slope for 3 out of 4 data sets (Figs. 8.9, 8.10). The model 2 fit for the data set from CAGEAN ages 3-17 was highly nonlinear with decreasing slope as predicted by a type II functional response (Fig. 8.9 B). Model 3 fits were dome shaped for two of the data sets (CAGEAN ages 6-10, Fig. 8.9 A; VPA ages 3-17, Fig. 8.9 D), although the dome shape for the CAGEAN data set occurred outside the range of the data (Fig. 8.9 A). The other two fits of model 3 were nearly linear with decreasing slope and very similar to model 2 fit for data from CAGEAN ages 3-17 (Fig. 8.9). The

Table 8.5. Summary statistics for single species mortality model fits to English sole data sets. From left to right are the data source (age range and method), model number ($Y=\bar{Y}$ denotes fitting data with mean \bar{Y} , 1=linear, 2=disc, 3=generalized equation), the parameter values a , b , and c as appropriate, the P values for the test of $H_0: b=0$ for the linear model, the power for the same test, the residual sums of squares (SSE), the coefficient of determination (r^2), the degrees of freedom (df; $n=25$ for CAGEAN and 24 for VPA), the residual mean square error (MSE), the F value for test of the significance of the fit, and the P value. Note: — indicates F and P value not computed because SSE of model was greater than or equal to SSE of $Y=\bar{Y}$.

Data source	Model	Parameters			$P(b b=0)$	Power	SSE	r^2	df	MSE	F	P
		a	b	c								
Ages	$Y=\bar{Y}$						52.72		23	2.29		
6-10	1	2.27	-1.51E-4		0.82	0.04	52.59	0.00	22	2.39	0.05	0.83
CAG	2	32807	14570				52.61	0.00	22	2.39	0.05	0.83
	3	2128	14000	-0.01			65.16	—	21	3.10	—	—
Ages	$Y=\bar{Y}$						65.63		22	2.98		
6-10	1	2.66	-3.54E-4		0.57	0.08	64.61	0.02	21	3.08	0.33	0.57
VPA	2	13710	4995				64.71	0.01	21	3.08	0.30	0.59
	3	5641	2482	-5.33E-5			64.62	0.02	20	3.23	0.31	0.74
Ages	$Y=\bar{Y}$						10.88		23	0.47		
3-17	1	1.55	-0.00011		0.30	0.17	10.34	0.05	22	0.47	1.15	0.30
CAG	2	4530	-487				10.13	0.07	22	0.46	1.63	0.22
	3	4528	-2519	-3.30E-4			10.09	0.07	21	0.48	1.64	0.22
Ages	$Y=\bar{Y}$						8.15		22	0.37		
3-17	1	1.00	-0.00002		0.80	0.04	8.13	0.00	21	0.39	0.06	0.81
VPA	2	53809	55195				8.13	0.00	21	0.39	0.05	0.83
	3	5912	85235	-9.79E-4			7.72	0.05	20	0.39	1.11	0.35

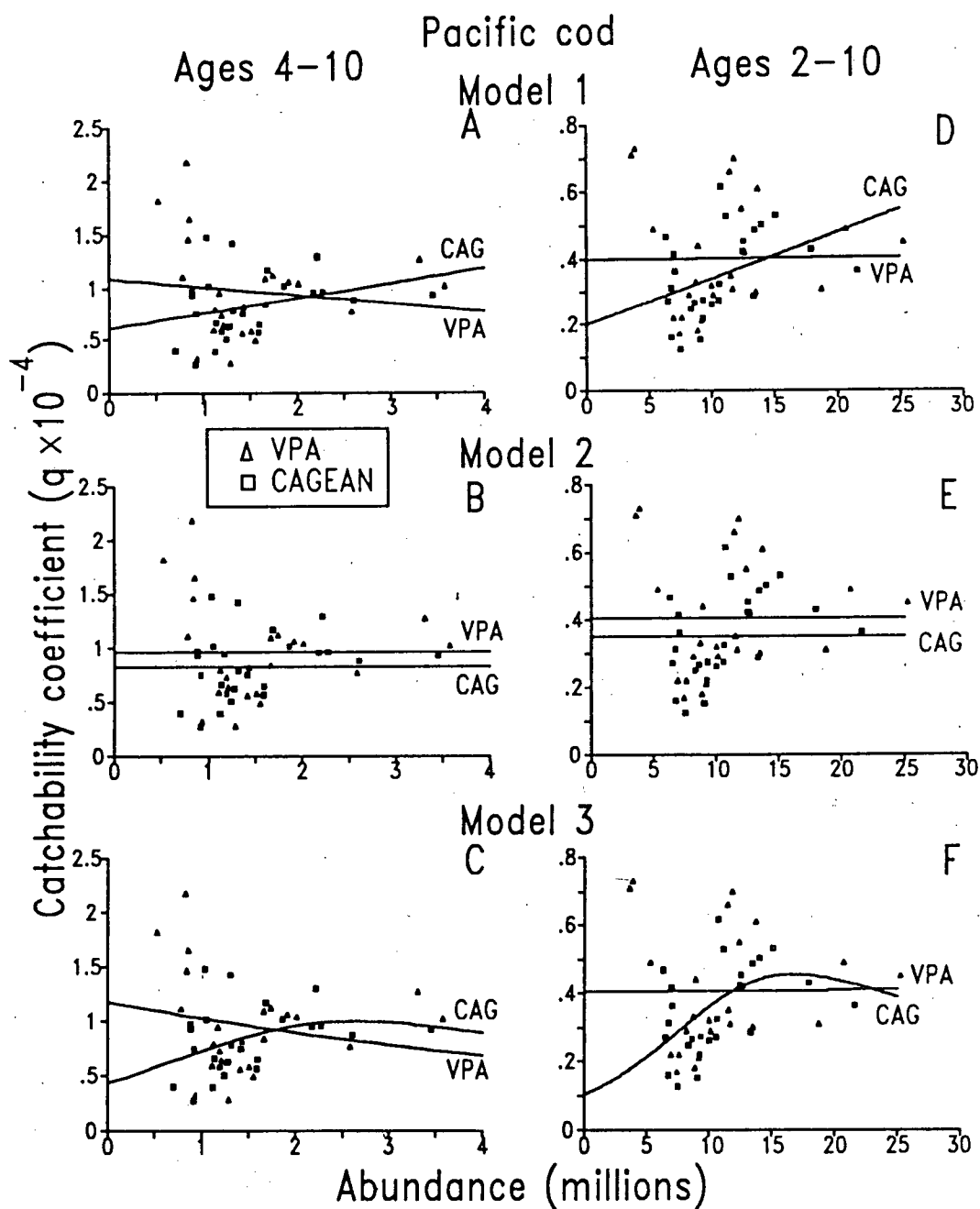


Figure 8.8. Comparison of alternative single species mortality models from VPA and CAGEAN fit to data sets for Pacific cod. Squares and triangles are observations from CAGEAN and VPA. Predicted lines are drawn using the best fit parameters (Table 8.4). Labels beside lines (VPA and CAG) denote catch-at-age method. Model numbers are indicated above each pair of horizontal panels. Panels A , B and C use data sets for ages 4-10 and panels D, E and F use data sets for ages 2-10.

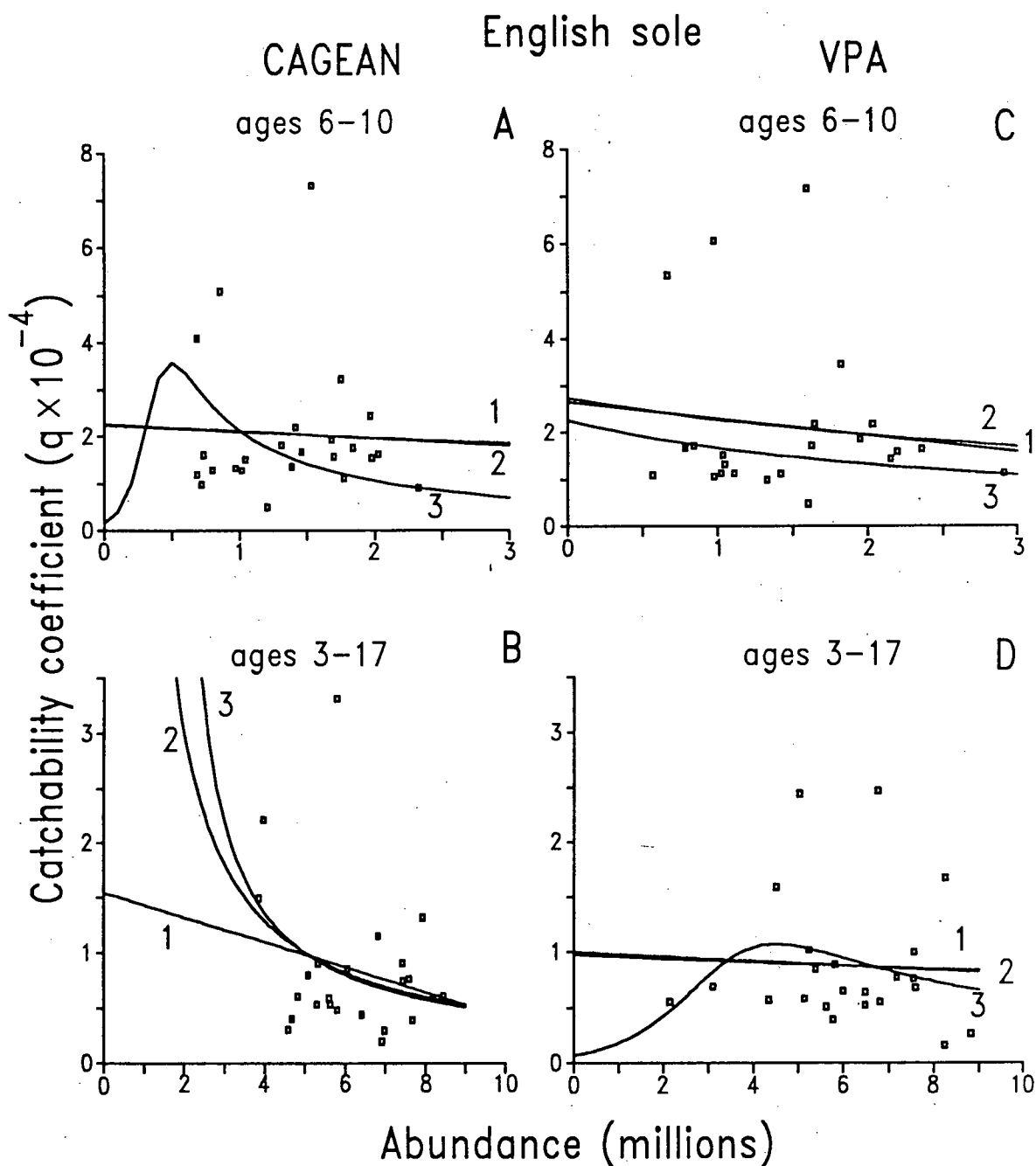


Figure 8.9. Comparison of alternative single species mortality model fits to English sole data sets. Squares are observations and predicted lines were drawn using the best fit parameters (Table 8.5). Numbers beside lines denote the model number; 1=linear, 2=disc, 3=generalized equation. Panels A and B use data sets from CAGEAN for ages 6-10 and 3-17 and panels C and D use data sets from VPA for the same age ranges.

predicted mortality curves were similar for data from VPA and CAGEAN for half of the data set-model combinations (models 1,2 ages 6-10, and model 1 ages 3-17; Fig. 8.10 A, B, and D). However, all comparisons should be interpreted cautiously given the similar SSE values and low r^2 s for all three models when fit to each data set.

The mortality curves were generally consistent with the predicted functional response for each model and data set with the exception that mortality curve for the VPA (ages 3-17) data set was linear and the functional response was saturating (cf. Figs. 8.4 and 8.10).

Rock sole

As found for the other two species, the alternative mortality models fit the rock sole data sets poorly; none of the fits were statistically significant (all r^2 s ≤ 0.07 , $P \geq 0.25$; Table 8.6). For the linear model the null hypothesis of $b = 0$ was not rejected for any of the data sets and power was low (≤ 0.17 ; Table 8.6). Thus it would be incorrect to conclude that q is density independent.

Mortality curves predicted by model 2 fits were equivalent to fitting $q =$ constant for all data sets (Fig. 8.11). Curves for model 3 fits were nearly linear with increasing slope for 3 of the data sets and dome shaped for the data from CAGEAN (ages 4-15; Fig 8.11 B).

Mortality curves fit to data from VPA and CAGEAN were similar for all model/age range combinations with the exception of model 3 fit to data from ages 4-15, where the best fit to CAGEAN data was dome shaped and the VPA curve was nearly linear (Fig. 8.12 B and D). Given the low r^2 s, it is highly

Table 8.6. Summary statistics for single species mortality model fits to rock sole data sets. From left to right are the data source (age range and method), model number ($Y=\bar{Y}$ denotes fitting data with mean Y , 1=linear, 2=disc, 3=generalized equation), the parameter values a , b , and c as appropriate, the P values for the test of $H_0: b=0$ for the linear model, the power for the same test, the residual sums of squares (SSE), the coefficient of determination (r^2), the degrees of freedom (df; $n=25$ for CAGEAN and 24 for VPA), the residual mean square error (MSE), the F value for test of the significance of the fit, and the P value. Note: — indicates F and P value not computed because SSE of model was greater than or equal to SSE of $Y=\bar{Y}$.

Data source	Model	a	b	c	$P(b=0)$	Power	SSE	r^2	df	MSE	F	P
Ages 6-10	$Y=\bar{Y}$						86.38		22	3.93		
CAG	1	1.59	7.72E-4		0.31	0.17	82.16	0.05	21	3.91	1.08	0.31
	2	2.50E+7	9.29E+6				86.39	—	21	4.11	—	—
	3	9.17E+6	5.85E+6	-3.60E-4			81.49	0.06	20	4.07	1.20	0.32
Ages 6-10	$Y=\bar{Y}$						223.26		21	10.63		
VPA	1	1.72	9.96E-4		0.35	0.15	213.65	0.04	20	10.68	0.90	0.35
	2	1.90E+8	5.76E+7				223.26	0.00	20	11.16	0.00	1.00
	3	2.18E+7	1.52E+7	-4.85E-4			207.13	0.07	19	10.90	1.48	0.25
Ages 4-15	$Y=\bar{Y}$						20.37		22	0.93		
CAG	1	0.96	9.54E-5		0.51	0.09	19.95	0.02	21	0.95	0.44	0.51
	2	1.91E+7	1.41E+7				20.37	0.00	21	0.97	0.00	1.00
	3	9648	51711	-7.80E-4			19.04	0.07	20	0.95	1.40	0.27
Ages 4-15	$Y=\bar{Y}$						38.04		21	1.81		
VPA	1	0.90	1.38E-4		0.41	0.12	36.74	0.03	20	1.84	0.71	0.41
	2	2.11E+8	1.38E+8				38.04	0.00	20	1.90	0.00	1.00
	3	3.28E+7	2.98E+7	-7.08E-5			37.01	0.03	19	1.95	0.53	0.60

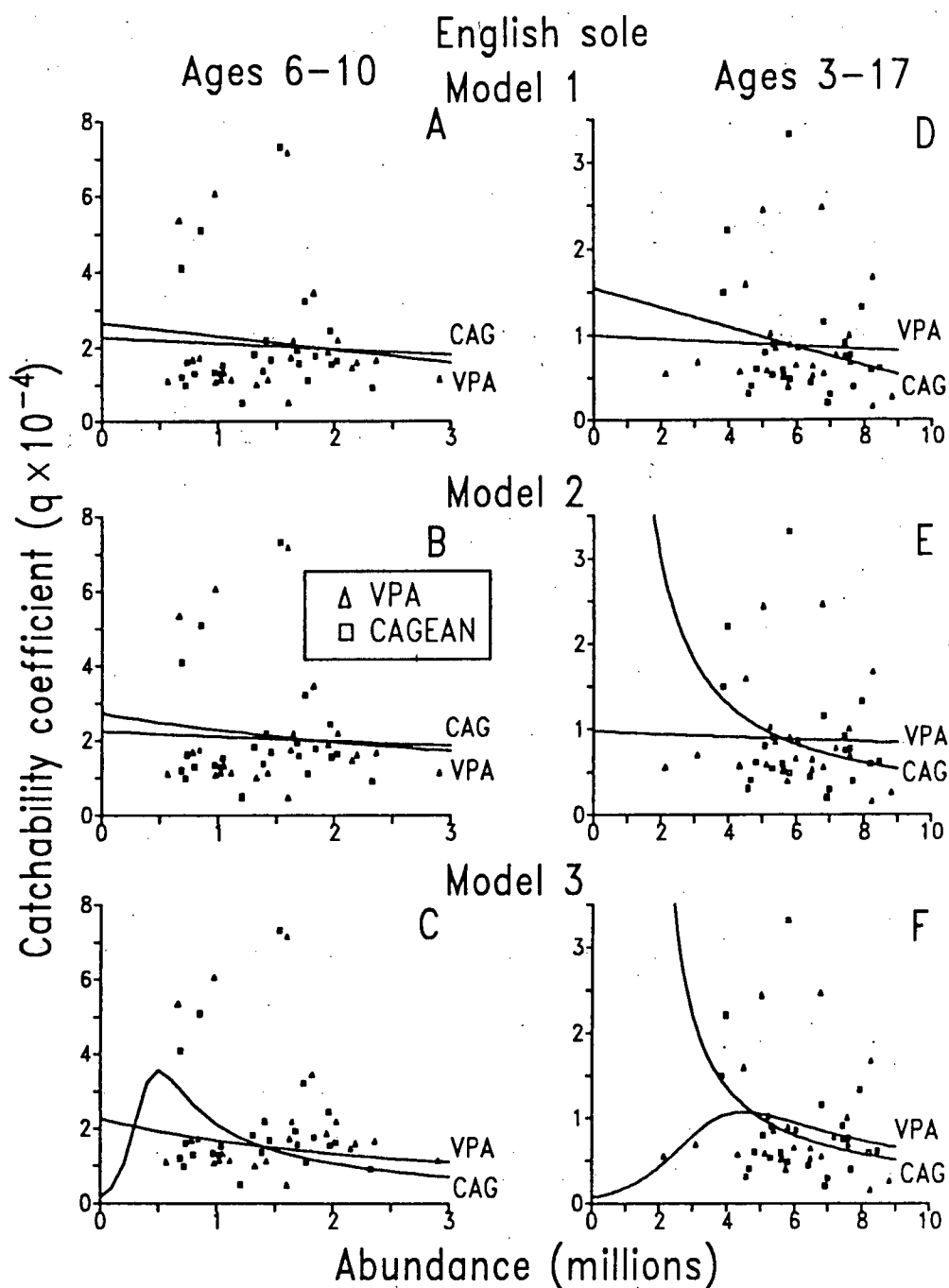


Figure 8.10. Comparison of alternative single species mortality models from VPA and CAGEAN fit to data sets for English sole. Squares and triangles are observations from CAGEAN and VPA. Predicted lines are drawn using the best fit parameters (Table 8.5). Labels beside lines (VPA and CAG) denote catch-at-age methods. Model numbers are indicated above each pair of horizontal panels. Panels A, B and C use data sets for ages 6-10 and panels D, E and F use data sets for ages 3-17.

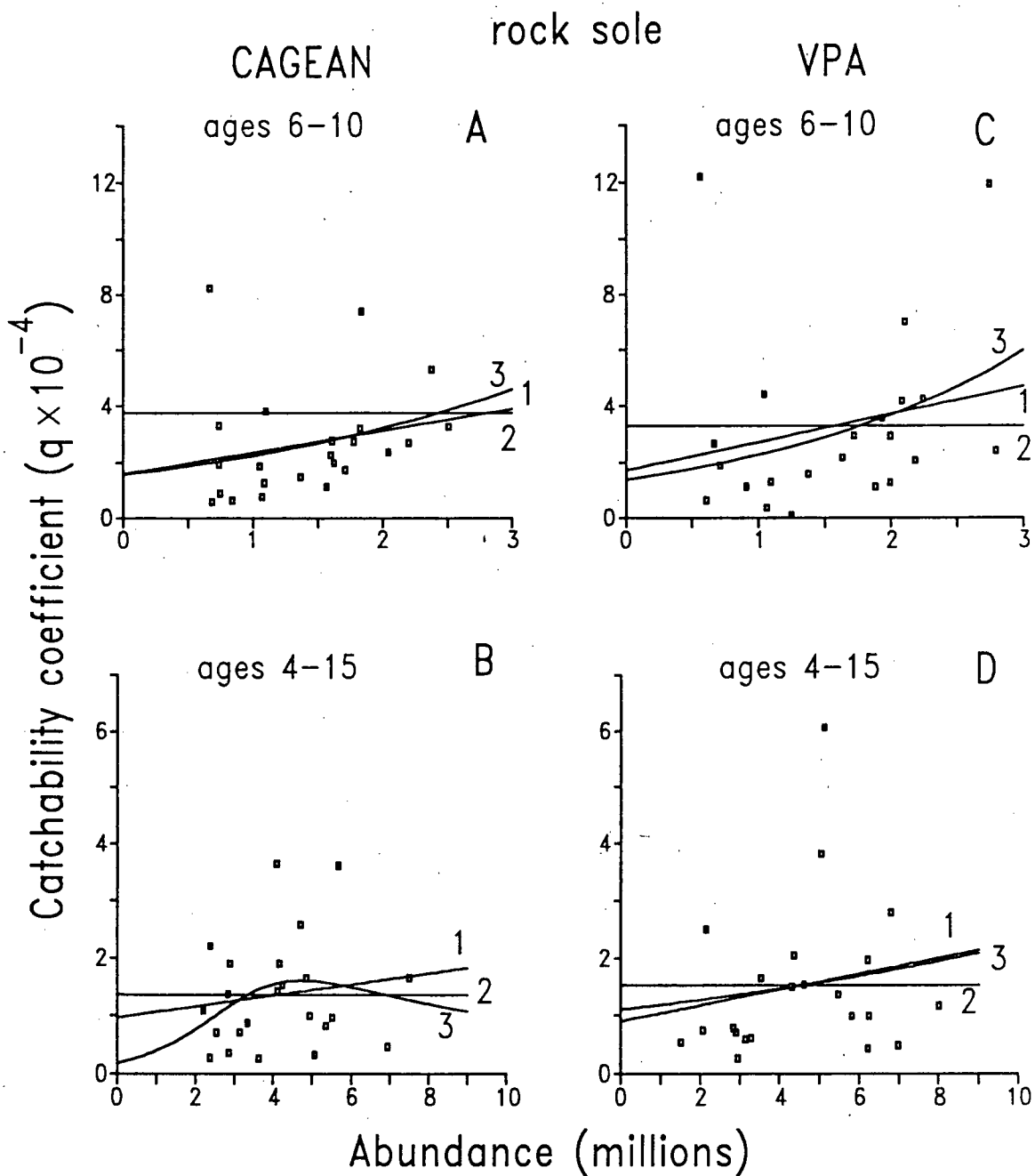


Figure 8.11. Comparison of alternative single species mortality model fits to rock sole data sets. Squares are observations and predicted lines were drawn using the best fit parameters (Table 8.6). Numbers beside lines denote the model number; 1=linear, 2=disc, 3=generalized equation. Panels A and B use data sets from CAGEAN for ages 6-10 and 4-15 and panels C and D use data sets from VPA for the same age ranges.

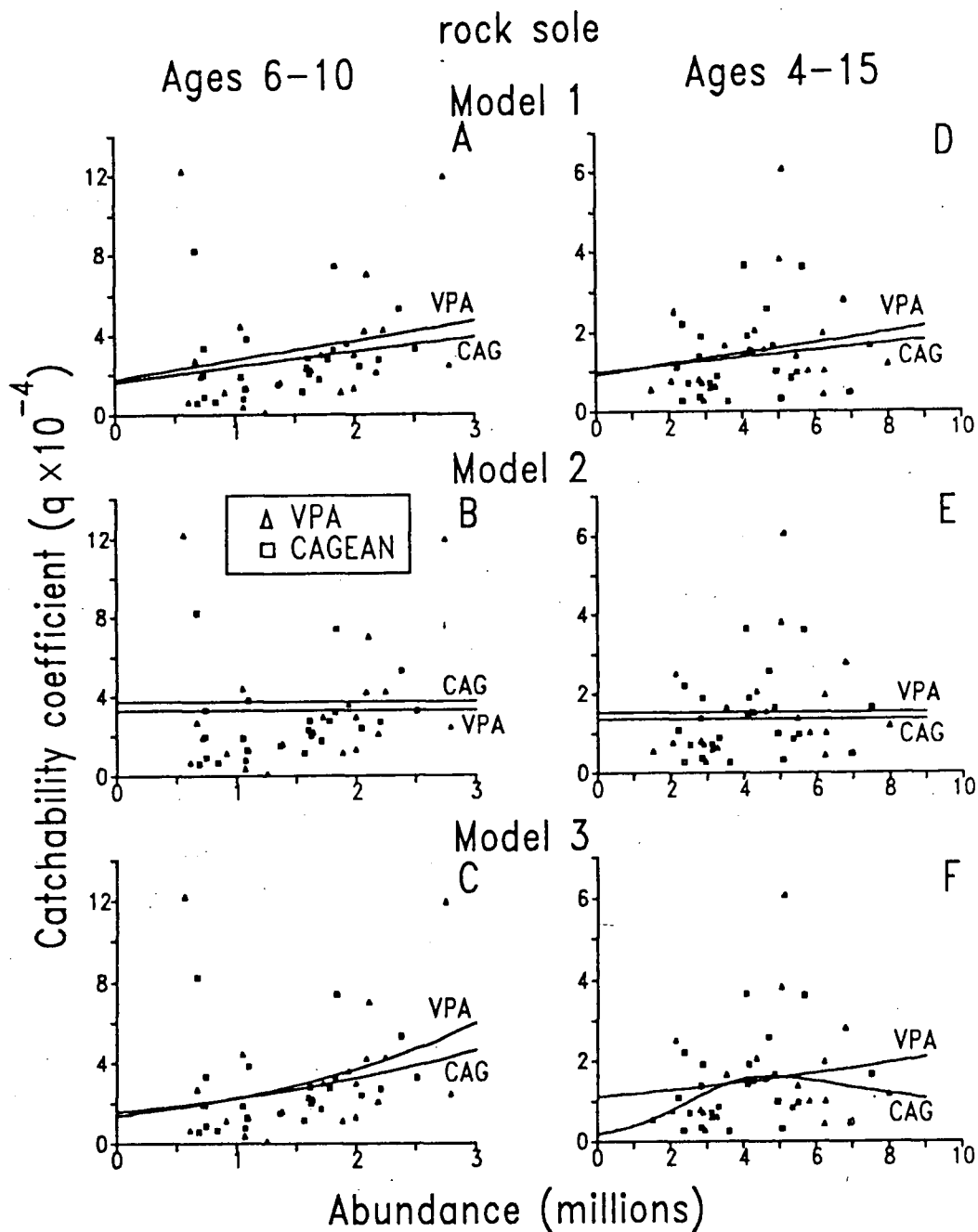


Figure 8.12. Comparison of alternative single species mortality models from VPA and CAGEAN fit to data sets for rock sole. Squares and triangles are observations from CAGEAN and VPA. Predicted lines are drawn using the best fit parameters (Table 8.6). Labels beside lines (VPA and CAG) denote catch-at-age methods. Model numbers are indicated above each pair of horizontal panels. Panels A, B and C use data sets for ages 6-10 and panels D, E and F use data sets for ages 4-15.

unlikely that these qualitative differences would be quantitatively significant.

Mortality curves were generally qualitatively consistent with the functional response curves for each data set with the exception of the data set for VPA ages 4-15 where the mortality curve was linear and the functional response was sigmoid (cf. Figs. 8.6 and 8.12).

Multispecies Functional Response Models

Pacific cod

Both the multispecies disc equation (MSDE; eq. 8.6, p. 223) and the linear model fit the cod data sets very well (all r^2 s ≥ 0.73 , $P \leq 0.0003$; Table 8.7). For a given data set, fits of the linear and MSDE models had very similar r^2 s and for a given catch-at-age method, fits of both models to data sets for the two age ranges had virtually identical r^2 s (Table 8.7). However, for a given age range, fits were consistently better for VPA data sets than for CAGEAN data sets (Table 8.7). The distributions of residuals were significantly non normal for fits of both models to the CAGEAN data set that used all ages and for the MDSE fit to the VPA data set for all ages (Table 8.7).

The general form of the functional response predicted by the MDSE was that cod LPE increased nearly linearly with increases its own abundance (e.g. Fig. 8.13). This pattern was consistent among all data sets. However, the effect of alternative prey abundance on cod LPE varied among data sets for the two age ranges. For data sets from fully recruited ages, cod LPE decreased with increases in alternative prey abundance but for data sets from all ages cod LPE increased (Table 8.7). The b parameter of the linear model was positive and the

Table 8.7. Summary statistics for multispecies functional response model fits to Pacific cod data sets. From left to right are the data source (age range and method), model type ($Y=\bar{Y}$ denotes fitting data with mean Y), the parameter values a , b , c and d , the residual sums of squares (SSE), the coefficient of determination (r^2), the degrees of freedom (df; $n=18$), the residual mean square error (MSE), the F statistics for the significance of the fits and corresponding P values and for tests of the normality of residuals, Stephens' (1974) modified A^2 statistic and corresponding P value.

Data source	model	Parameters				SSE	r^2	df	MSE	F	Normality		
		a	b	c	d						P	modified A^2	P
ages	$Y=\bar{Y}$					39992		17	2352				
4-10	linear	6.34	0.060	-0.022	7.31E-3	9343	0.77	14	667	15.31	<0.001	0.50	>0.15
CAG	MSDE	0.069	4.05E-5	2.57E-4	-8.80E-5	10626	0.73	14	759	12.90	0.0003	0.59	>0.10
ages	$Y=\bar{Y}$					55393		17	3258				
4-10	linear	-17.05	0.057	-0.025	0.027	8553	0.85	14	611	25.56	<0.001	0.34	>0.15
VPA	MSDE	0.048	4.28E-5	2.78E-4	-3.06E-4	9302	0.83	14	644	23.12	<0.001	0.41	>0.15
ages	$Y=\bar{Y}$					425700		17	25041				
2-10	Linear	-168.02	0.032	2.77E-3	0.018	96672	0.77	14	6905	15.88	<0.001	1.01	<0.01
CAG	MSDE	0.019	-2.18E-6	-1.59E-5	-2.67E-5	115634	0.73	14	8260	12.51	0.0003	0.99	<0.01
ages	$Y=\bar{Y}$					690990		17	40646				
2-10	Linear	-285.58	0.028	0.068	-0.025	99599	0.86	14	7114	27.71	<0.001	0.35	>0.15
VPA	MSDE	0.016	3.14E-6	-1.16E-4	5.65E-5	119547	0.83	14	8539	22.31	<0.001	0.87	<0.025

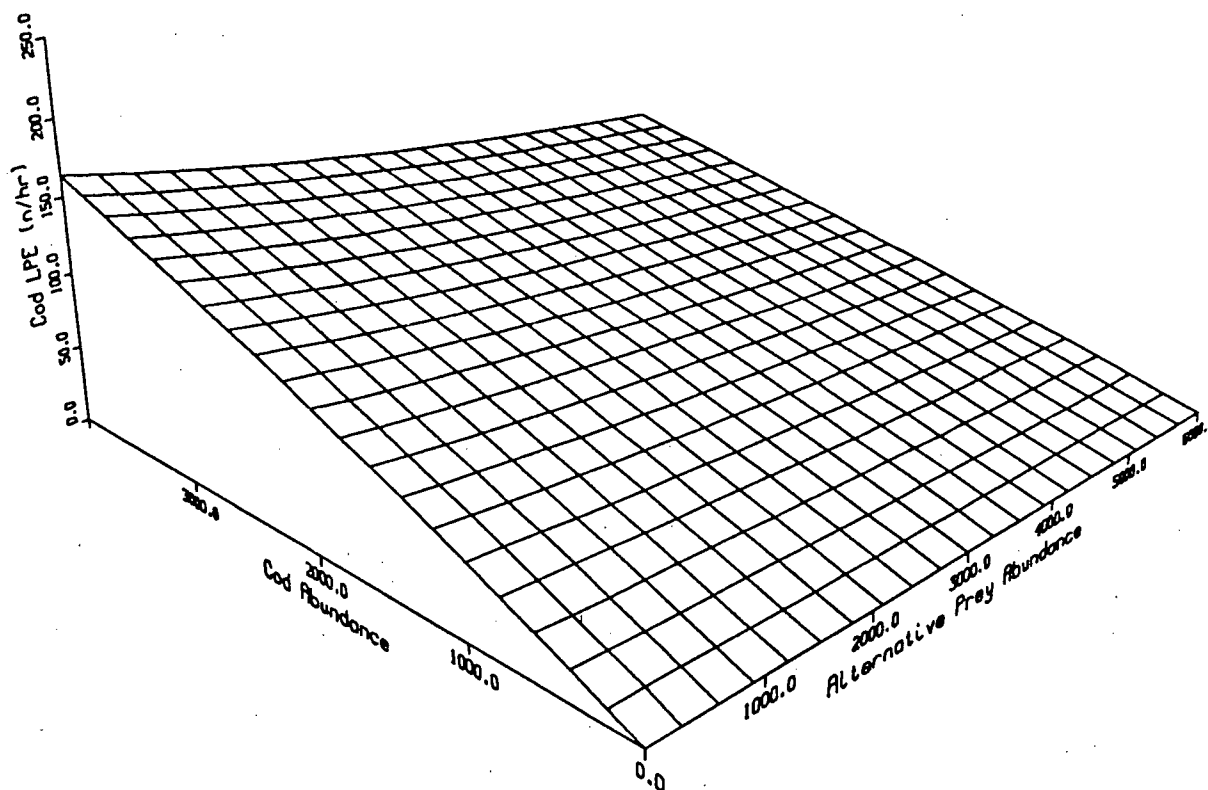


Figure 8.13. Predicted multispecies functional response surface for Pacific cod using the data set from VPA for ages 4-10. Alternative prey abundance is English sole plus rock sole abundance for fully recruited ages (6-10) estimated by VPA. Abundance is in thousands of fish. Parameter estimates and other statistics are given in Table 8.7.

c and d parameters of the MSDE and linear models were opposite in sign for all data sets (Table 8.7). Thus, the linear and MDSE models predicted similar qualitative forms of multispecies responses.

The form of the multispecies models was generally consistent with the form found for the single species models which also showed very little evidence for an asymptote (cf. Figs. 8.1 and 8.13). The fits of the multispecies models

had slightly higher r^2 s than the fits of the single species models in some cases (cf. Tables 8.1 and 8.7). However, because of differences in data sets (i.e. the multispecies models were fit to 1961-78 vs. 1961-85 for the single species models), the relative merits of single species vs. multispecies models cannot be determined.

English sole

Both the MDSE and linear model fit the English sole data sets for fully recruited ages better than data sets for all ages ($0.41 \leq r^2 \leq 0.86$, $P \leq 0.051$ vs. $0.08 \leq r^2 \leq 0.17$, $P \geq 0.45$; Table 8.8). The MDSE fit better for 3 out of 4 data sets (Table 8.8). Both models fit the VPA data sets better than the CAGEAN data sets (Table 8.8). In all cases, the distributions of residuals were not significantly different from normal (Table 8.8).

The general form of the multispecies responses for English sole was that LPE increased with increased in English sole abundance and decreased slightly as the abundance of alternative prey increased (e.g. Fig. 8.14). The b parameter of the linear model was positive and the c and d parameters of the MDSE and linear models were opposite in sign for 3 out of 4 data sets (Table 8.8). Thus, in most cases, the linear and MSDE models predicted similar qualitative forms for the functional response. r^2 s for both multispecies models were higher than r^2 s for single species models for data sets that used fully recruited ages, but were similar for data sets that used all ages (cf. Table 8.2 and 8.8).

Table 8.8. Summary statistics for multispecies functional response model fits to English sole data sets. From left to right are the data source (age range and method), model type ($Y=\bar{Y}$ denotes fitting data with mean \bar{Y}), the parameter values a , b , c and d , the residual sums of squares (SSE), the coefficient of determination (r^2), the degrees of freedom (df; $n=18$), the residual mean square error (MSE), the F statistics for the significance of the fits and corresponding P values and for tests of the normality of residuals, Stephens' (1974) modified A^2 statistic and corresponding P value.

Data source	model	Parameters				SSE	r^2	df	MSE	F	P	Normality	
		a	b	c	d							modified A^2	P
ages	$Y=\bar{Y}$					74411		17	4377				
6-10	linear	72.44	0.067	-0.042	0.040	43538	0.41	14	3110	3.31	0.051	0.61	>0.05
CAG	MSDE	0.19	5.50E-4	4.66E-4	-5.31E-4	32367	0.57	14	2312	6.06	0.007	0.39	>0.15
ages	$Y=\bar{Y}$					138620		17	8154				
6-10	linear	67.20	0.045	-0.066	0.083	32644	0.76	14	2332	5.97	0.008	0.34	>0.15
VPA	MSDE	0.20	3.93E-4	7.52E-4	-5.42E-4	19281	0.86	14	1377	28.88	<0.0001	0.34	>0.15
ages	$Y=\bar{Y}$					314730		17	18514				
3-17	linear	320.75	0.021	-0.011	-3.89E-3	282690	0.10	14	20192	0.53	0.67	0.33	>0.15
CAG	MSDE	8386.	17.85	6.04	-1.44	290714	0.08	14	20765	0.39	0.76	0.42	>0.15
ages	$Y=\bar{Y}$					628290		17	36958				
3-17	linear	380.37	-0.017	-0.010	0.038	559770	0.11	14	39984	0.57	0.64	0.59	>0.10
VPA	MSDE	188.13	0.71	0.10	-0.42	522798	0.17	14	37343	0.94	0.45	0.61	>0.05

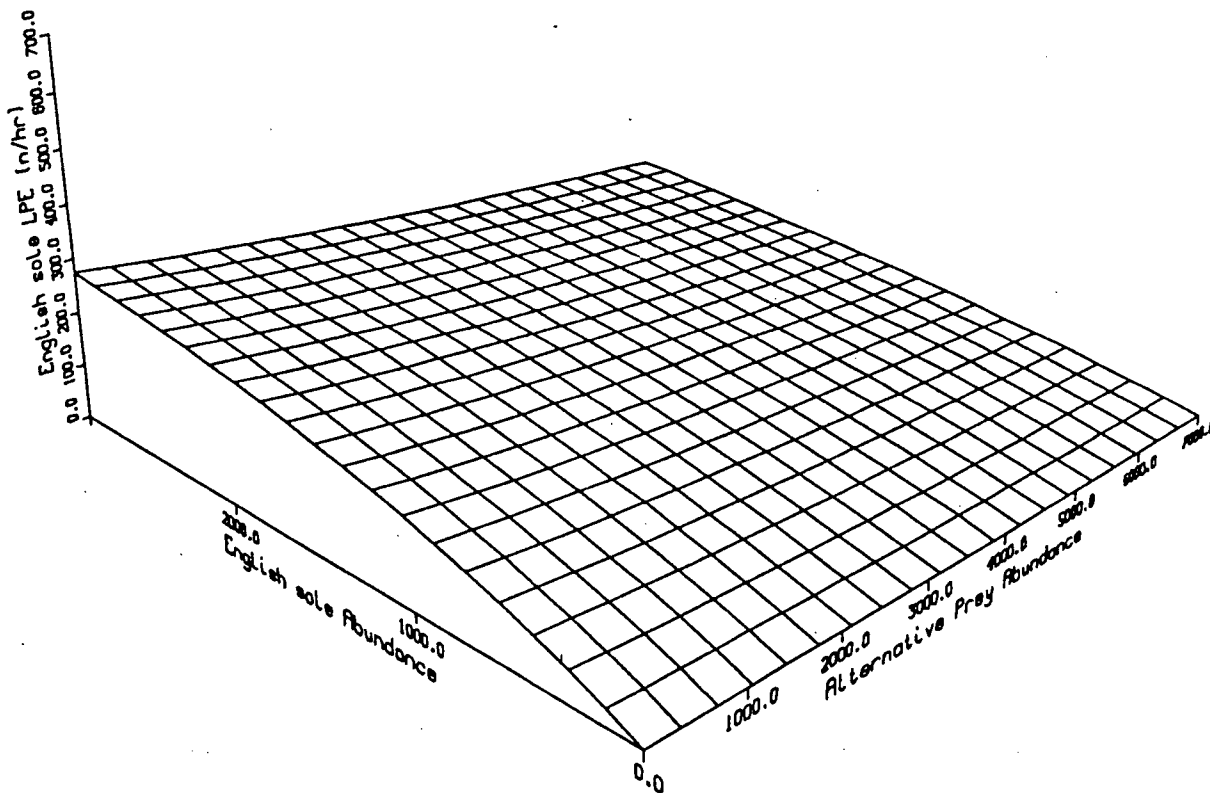


Figure 8.14. Predicted multispecies functional response surface for English sole using the data set from VPA for ages 6-10. Alternative prey is cod abundance plus rock sole for fully recruited ages (4-10;6-10) estimated by VPA. Abundance is in thousands of fish. Parameter estimates and other statistics are given in Table 8.8.

Rock sole

Multispecies models fit rock sole data set reasonably well ($0.37 \leq r^2 \leq 0.79$, $P \leq 0.08$; Table 8.9). The MSDE fit better than the linear model for 3 out of 4 data sets and fits of both models to data sets that used fully recruited ages

Table 8.9. Summary statistics for multispecies functional response model fits to rock sole data sets. From left to right are the data source (age range and method), model type ($Y=\bar{Y}$ denotes fitting data with mean Y), the parameter values a , b , c and d , the residual sums of squares (SSE), the coefficient of determination (r^2), the degrees of freedom (df; $n=18$), the residual mean square error (MSE), the F statistics for the significance of the fits and corresponding P values and for tests of the normality of residuals, Stephens' (1974) modified A^2 statistic and corresponding P value.

Data source	model	Parameters				SSE	r^2	df	MSE	F	Normality		
		a	b	c	d						P	modified A^2	P
ages	$Y=\bar{Y}$					1269200		17	74659				
6-10	linear	-131.08	0.39	-0.066	-0.037	492500	0.61	14	35179	7.36	0.003	1.70	<0.01
CAG	MSDE	0.087	-3.49E-4	9.59E-5	-5.32E-5	381942	0.70	14	27282	10.84	0.0006	2.50	<0.01
ages	$Y=\bar{Y}$					5068800		17	298165				
6-10	linear	90.59	0.69	-0.28	-0.28	1777800	0.65	14	126986	8.64	0.002	0.92	<0.025
VPA	MSDE	-1384.	3.07	-12.36	0.47	1073768	0.79	14	76698	17.36	<0.0001	1.14	<0.01
ages	$Y=\bar{Y}$					2385400		17	140318				
4-15	linear	528.74	0.14	-0.019	-0.082	1391000	0.42	14	99357	3.34	0.05	1.04	<0.01
CAG	MSDE	42.11	-0.056	8.31E-3	0.10	1386544	0.42	14	99039	3.36	0.05	1.11	<0.01
ages	$Y=\bar{Y}$					5860900		17	344759				
4-15	linear	489.94	0.27	-0.020	-0.16	3670600	0.37	14	262186	2.78	0.08	1.54	<0.01
VPA	MSDE	-8.53E-3	-8.14E-4	3.21E-5	5.70E-4	2546866	0.57	14	181919	6.07	0.007	1.64	<0.01

were better than fits to data sets that included all ages (Table 8.9). Fits to VPA data sets were better than fits to CAGEAN data sets with one exception (the linear model fit to data from all ages; Table 8.9). As found for single species responses, distributions of residuals from fits of both models to rock sole data sets were significantly non normal ($P < 0.025$; Table 8.9).

The general form of multispecies response found for rock sole was that LPE increased with increases in rock sole abundance but decreased with increases in alternative prey abundance (e.g. Fig. 8.15). The qualitative form of the response was consistent for all data sets. The b parameter of the linear model was positive for all data sets and the c and d parameters of the MSDE and linear models were opposite in sign for 6 of 8 comparisons (Table 8.9). Thus in most cases, the MSDE and linear models predicted similar qualitative forms of response. For a given data set, r^2 values were consistently higher for the multispecies models when compared to single species models (cf. Tables 8.3 and 8.9).

Multispecies Mortality Curves

Pacific cod

Both of the multispecies mortality models generally fit the cod data sets better than the single species models ($0.18 \leq r^2 \leq 0.58$, Table 8.10; cf. Table 8.4). For a given data set, the MSDE and linear models had similar r^2 s. For a given catch-at-age method, fits were better for data sets using all ages than for data sets using fully recruited ages, and for a given age range, fits were better for VPA data sets than for CAGEAN data sets (Table 8.10).

Table 8.10. Summary statistics for multispecies mortality model fits to Pacific cod data sets. From left to right are the data source (age range and method), model type (Y=Y denotes fitting data with mean Y), the parameter values *a*, *b*, *c* and *d*, the residual sums of squares (SSE), the coefficient of determination (r^2), the degrees of freedom (df; n=18), the residual mean square error (MSE), the F statistics for the significance of the fits and corresponding P values.

Data source	model	Parameters				SSE	r^2	df	MSE	F	P
		<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>						
Ages	Y=Y					1.80		17	0.11		
4-10	linear	0.79	1.28E-4	-2.12E-4	1.00E-4	1.43	0.20	14	0.10	1.20	0.35
CAG	MSDE	0.92	-6.49E-5	2.88E-4	-1.25E-4	1.48	0.18	14	0.11	1.01	0.42
Ages	Y=Y					3.66		17	0.22		
4-10	linear	0.76	-5.98E-5	-3.47E-4	4.40E-4	2.16	0.41	14	0.15	3.24	0.05
VPA	MSDE	0.81	9.16E-6	4.25E-4	-3.61E-4	1.72	0.53	14	0.12	5.27	0.01
Ages	Y=Y					0.30		17	0.02		
2-10	linear	0.08	1.01E-5	1.11E-5	2.62E-5	0.21	0.29	14	0.02	1.93	0.17
CAG	MSDE	0.23	-7.69E-6	-2.76E-5	-3.00E-5	0.24	0.22	14	0.02	1.29	0.32
Ages	Y=Y					0.45		17	0.03		
2-10	linear	-4.91E-3	3.61E-7	1.00E-4	-4.10E-5	0.22	0.52	14	0.02	5.02	0.01
VPA	MSDE	0.18	1.44E-5	-1.64E-4	6.43E-5	0.19	0.58	14	0.01	6.33	0.006

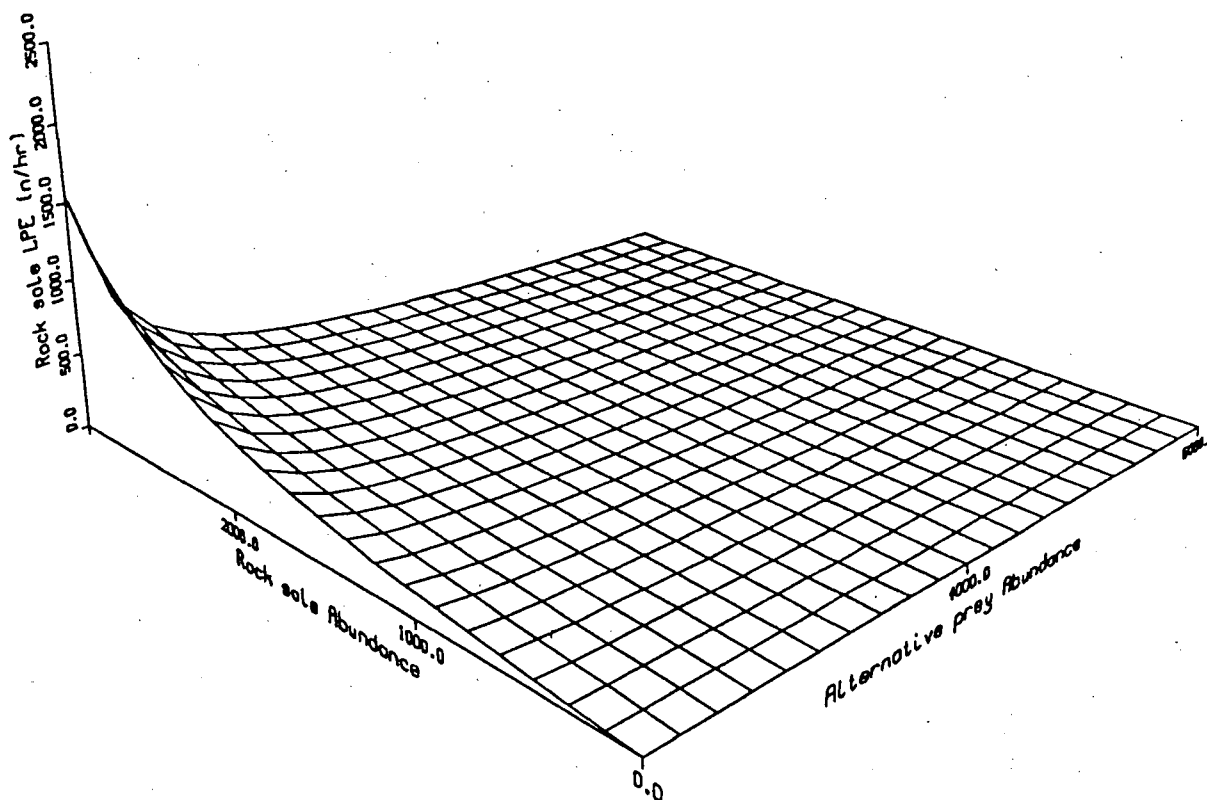


Figure 8.15. Predicted multispecies functional response surface for rock sole using the data set from VPA for ages 6-10. Alternative prey abundance is cod plus English sole abundance for fully recruited ages (4-10;6-10) estimated by VPA. Abundance is in thousands of fish. Parameter estimates and other statistics are given in Table 8.9.

The multispecies mortality curve for cod was a flat plane over most of the range of cod and alternative prey abundances for 3 out of 4 data sets (e.g. Fig. 8.16). However, for the VPA data set from all ages, catchability (q) increased sharply when very small cod abundances were coupled with very large abundances of alternative prey, and for the CAGEAN data set from fully recruited ages, q increased sharply as cod abundance increased and q decreased

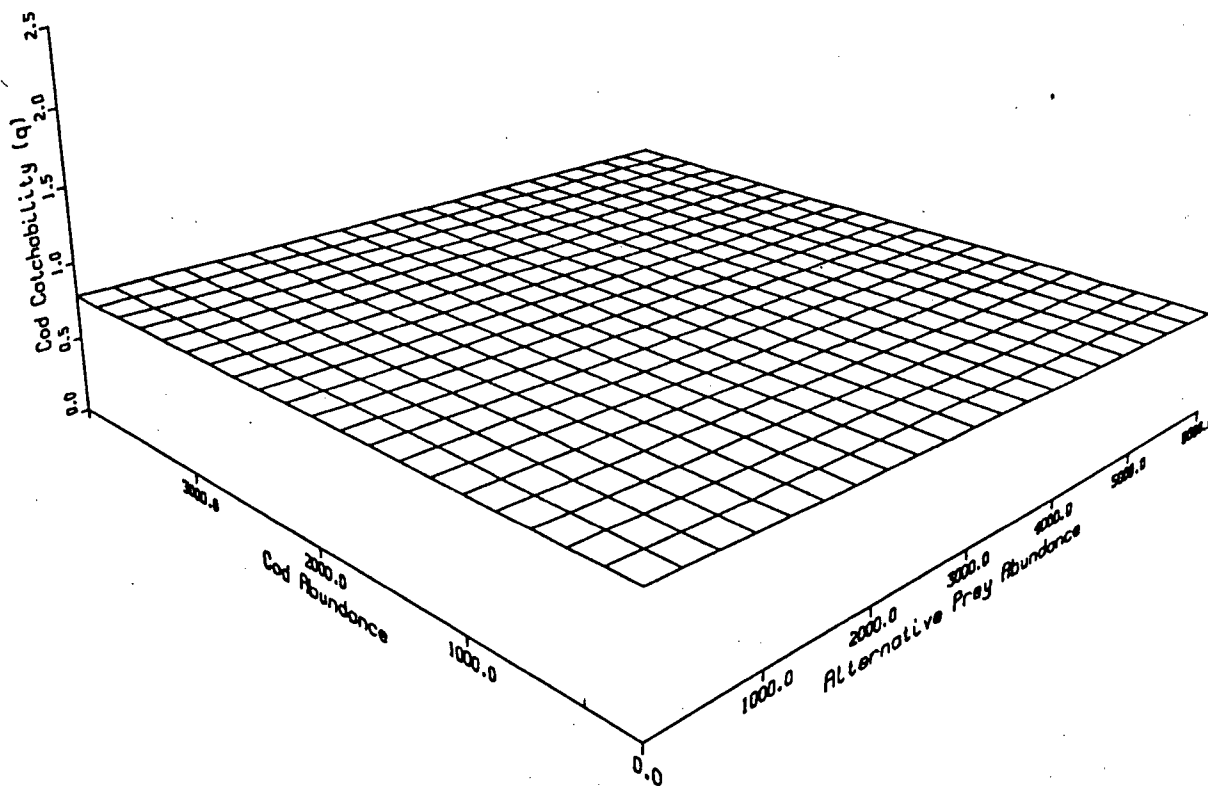


Figure 8.16. Predicted multispecies mortality response surface for Pacific cod using the data set from VPA for ages 4-10. Alternative prey abundance is English sole plus rock sole abundance for fully recruited ages (6-10) estimated by VPA. Abundance is in thousands of fish. Parameter estimates and other statistics are given in Table 8.10.

as the abundance of alternative prey increased. Note, however that the fit of the MDSE mortality model was not significant for the latter data set ($P=0.42$; Table 8.10). The b parameter of the linear model was small and the c and d parameters of the MSDE and linear model were opposite in sign for all data sets (Table 8.10). Thus, the MSDE and the linear model predicted similar qualitative forms of response. The form of the multispecies mortality response is

also consistent with the nearly linearly increasing multispecies functional response (Fig. 8.13) and with the single species mortality curves (cf. Figs. 8.7 and 8.13). The r^2 s for the multispecies mortality models were higher than those for the single species models for 3 out of 4 data sets (cf. Tables 8.4 and 8.10). Improvement in r^2 values was particularly striking for the VPA data sets (single species models: $0.0 \leq r^2 \leq 0.03$ vs. multispecies models: $0.41 \leq r^2 \leq 0.58$; Tables 8.4 and 8.10).

English sole

Both multispecies mortality models fit the English sole data sets much better than the single species models ($0.21 \leq r^2 \leq 0.94$, Table 8.11; cf. Table 8.5). The MSDE fit better than the linear model except for the VPA data set for all ages (where the r^2 s were identical; Table 8.11). Fits of both models to data sets that used fully recruited ages were better than fits to data sets that used all ages (Table 8.11).

The MSDE mortality curves for data sets that used fully recruited ages predicted that catchability decreased slightly with increases in English sole and alternative prey abundance (e.g. Fig. 8.17). However for data sets that used all ages, q decreased sharply with increases in English sole abundance for both VPA and CAGEAN data sets but was insensitive to changes in the abundance of alternative prey for the VPA data set and decreased sharply with increases in alternative prey for the CAGEAN data set. The b parameter for the linear model was negative for all data sets and the c and d parameters for the linear and MSDE were opposite in sign for data sets that used fully recruited ages, but had the same sign for data sets that used all ages. Thus, the linear model

Table 8.11. Summary statistics for multispecies mortality model fits to English sole data sets. From left to right are the data source (age range and method), model type ($Y=\bar{Y}$ denotes fitting data with mean Y), the parameter values a , b , c and d , the residual sums of squares (SSE), the coefficient of determination (r^2), the degrees of freedom (df; $n=18$), the residual mean square error (MSE), the F statistics for the significance of the fits and corresponding P values.

Data source	model	Parameters				SSE	r^2	df	MSE	F	P
		a	b	c	d						
Ages	$Y=\bar{Y}$					21.10		17	1.24		
6-10	linear	2.47	-5.62E-4	-7.83E-4	8.66E-4	11.30	0.46	14	.81	4.05	0.03
CAG	MSDE	2.36	5.24E-4	5.82E-4	-6.32E-4	4.38	0.79	14	.31	17.80	<0.001
Ages	$Y=\bar{Y}$					36.58		17	2.15		
6-10	linear	2.57	-1.22E-3	-1.14E-3	1.68E-3	8.62	0.76	14	.62	6.76	0.005
VPA	MSDE	3.15	7.27E-4	8.80E-4	-7.12E-4	2.27	0.94	14	.16	38.77	<0.001
Ages	$Y=\bar{Y}$					3.83		17	0.23		
3-17	linear	1.70	-1.10E-4	-3.07E-5	4.74E-6	2.89	0.24	14	0.21	1.51	0.26
CAG	MSDE	-0.45	-3.14E-4	-3.36E-5	6.60E-5	1.31	0.66	14	0.09	9.02	0.001
Ages	$Y=\bar{Y}$					4.66		17	0.27		
3-17	linear	1.48	-1.67E-4	-2.32E-5	1.15E-4	3.67	0.21	14	0.26	1.26	0.33
VPA	MSDE	-0.063	-2.32E-4	-1.89E-5	5.98E-5	3.70	0.21	14	0.26	1.21	0.34

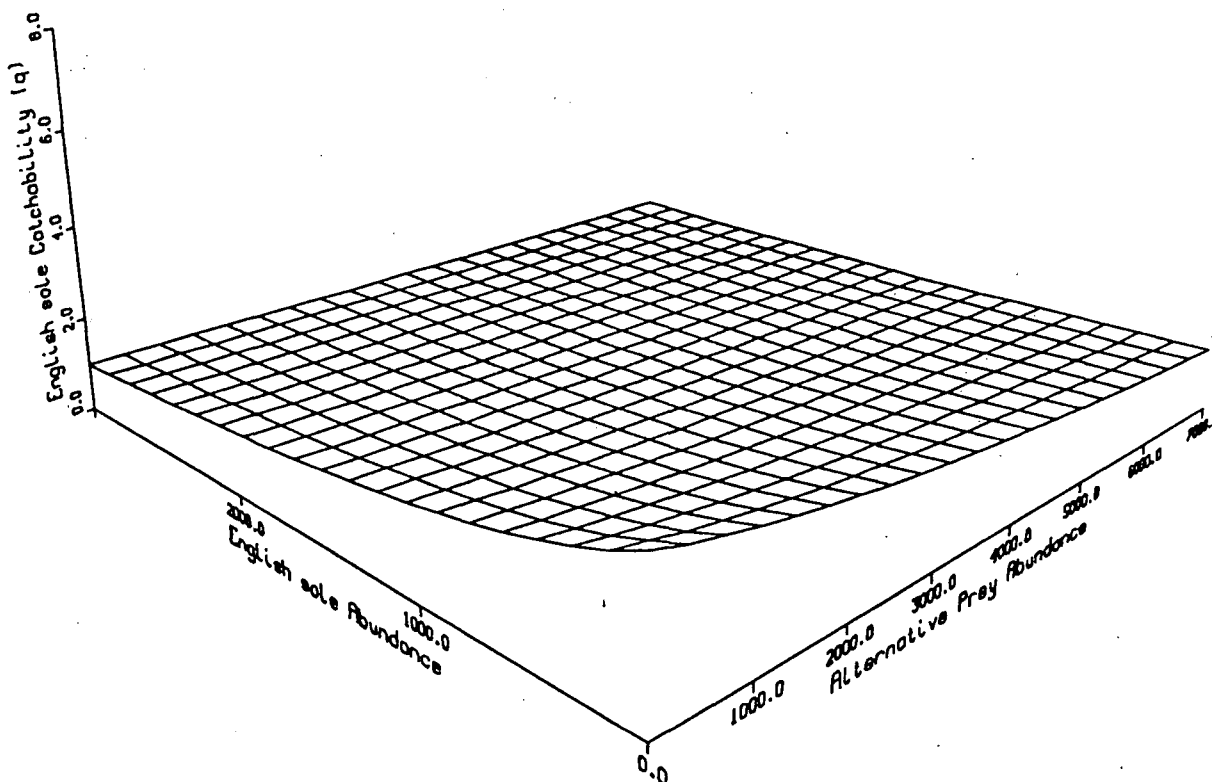


Figure 8.17. Predicted multispecies mortality response surface for English sole using the data set from VPA for ages 6-10. Alternative prey is cod plus rock sole abundance for fully recruited ages (4-10) estimated by VPA. Abundance is in thousands of fish. Parameter estimates and other statistics are given in Table 8.11.

and MSDE predicted the same qualitative form of response for data sets that used fully recruited ages, but they predicted opposite effects of alternative prey abundance for data sets that used all ages. In most cases, the form of the MSDE mortality curve was consistent with the single species fits (cf. Figs. 8.17 and 8.9).

Rock sole

As found for the other 2 species, multispecies mortality models fit the data sets for rock sole better than single species models (Table 8.12; cf. Table 8.6). Fits were better for data sets from fully recruited age ranges than for data sets using all ages for a given catch-at-age method and fits were better for VPA data sets than for CAGEAN data sets (Table 8.12).

Over most of the range of observed abundances the predicted mortality curve for rock sole was nearly flat, indicating density independent q (e.g. Fig. 8.18). However, the form of response varied among age ranges near the edge of the range of observed abundances for both rock sole and alternative prey. For data sets that used fully recruited ages, mortality curves predicted that q increased in response to increases in rock sole abundance and either decreased (VPA) or remained the same (CAGEAN) with increases in alternative prey abundance (e.g. Fig. 8.18). For data sets that used all ages, mortality curves predicted that q decreased with the abundance of alternative prey and increased with increases in rock sole abundance. The b parameter of the linear model was positive for all data sets, but the c and d parameters of the MSDE and linear models varied in sign. Thus, the linear model and MSDE predicted similar qualitative effects of rock sole abundance on q , but the predicted effects of alternative abundance on q varied among models and data sets. The multispecies mortality curves are consistent with the functional response curves because q is essentially the slope of LPE vs abundance (cf. Figs. 8.18 and 8.15).

Over most of the range of abundances the multispecies and single species mortality curves are consistent as both predict relatively flat or slightly

Table 8.12. Summary statistics for multispecies mortality model fits to rock sole data sets. From left to right are the data source (age range and method), model type ($Y=\bar{Y}$ denotes fitting data with mean Y), the parameter values a , b , c and d , the residual sums of squares (SSE), the coefficient of determination (r^2), the degrees of freedom (df; $n=18$), the residual mean square error (MSE), the F statistics for the significance of the fits and corresponding P values.

Data source	model	Parameters				SSE	r^2	df	MSE	F	P
Ages	$Y=\bar{Y}$					49.23		17	2.90		
6-10	linear	0.42	1.82E-3	-2.77E-4	-1.85E-4	32.08	0.35	14	2.29	2.49	0.10
CAG	MSDE	1.15	-3.26E-4	5.16E-5	-5.61E-5	31.98	0.35	14	2.28	2.52	0.10
Ages	$Y=\bar{Y}$					134.35		16	8.40		
6-10	linear	0.49	3.67E-3	-1.44E-3	-1.21E-3	50.88	0.62	13	3.91	7.11	0.005
VPA	MSDE	1.22	-3.71E-4	1.09E-4	2.95E-5	30.29	0.77	13	2.33	14.89	<0.001
Ages	$Y=\bar{Y}$					16.53		17	0.97		
4-15	linear	2.71	2.12E-4	-6.34E-5	-2.62E-4	11.30	0.32	14	0.81	2.16	0.14
CAG	MSDE	-7.89	9.36E-4	-1.88E-4	-1.66E-3	11.42	0.31	14	0.82	2.09	0.15
Ages	$Y=\bar{Y}$					29.38		16	1.84		
4-15	linear	3.07	5.96E-4	-3.35E-5	-6.66E-4	19.42	0.34	13	1.49	2.22	0.13
VPA	MSDE	28314	-10.59	-0.22	13.08	17.82	0.39	13	1.37	2.81	0.08

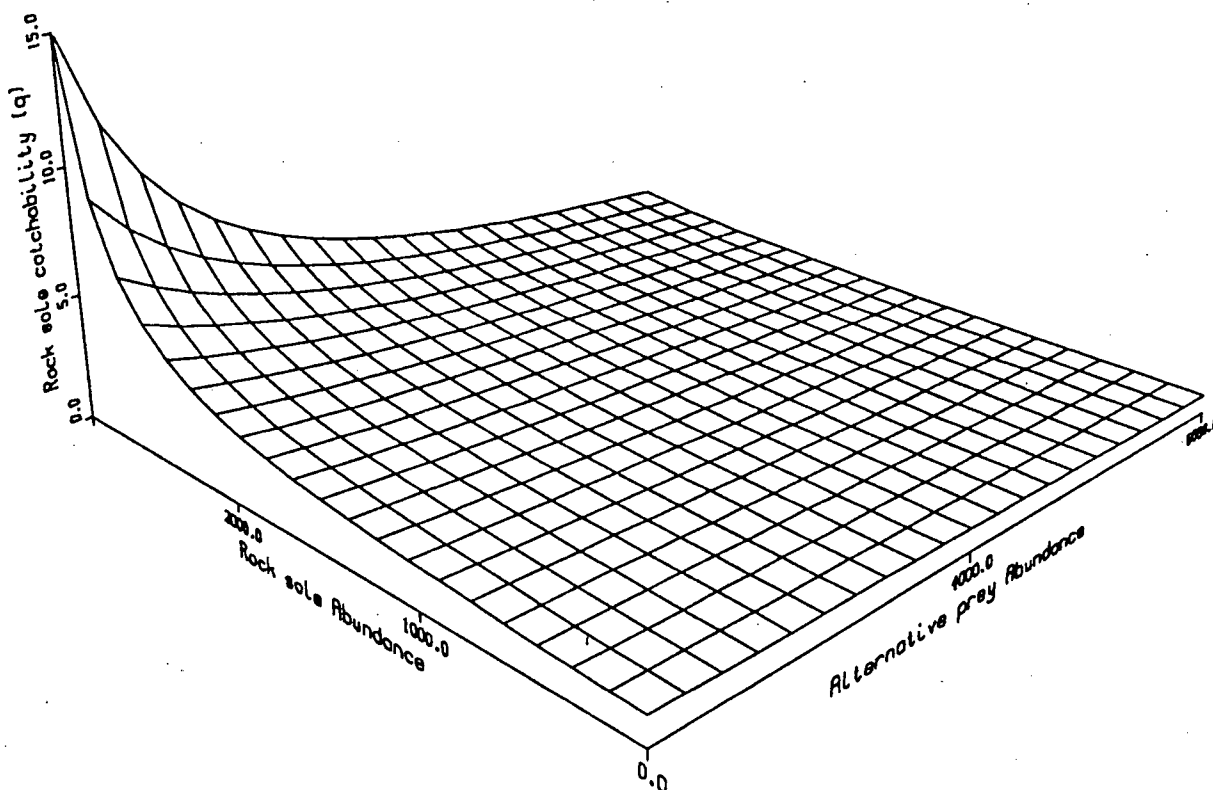


Figure 8.18. Predicted multispecies mortality response surface for rock sole using the data set from VPA for ages 6-10. Alternative prey abundance is cod plus English sole abundance for fully recruited ages (4-10;6-10) estimated by VPA. Abundance is in thousands of fish. Parameter estimates and other statistics are given in Table 8.12.

increasing curves (cf. Figs. 8.18, 8.12). The improvement in fit of multispecies models over single species models is particularly striking for the data set shown in figure 8.18 (i.e. ages 6-10 for VPA) where the best fit single species model had an r^2 of 0.07 compared with 0.77 for the MSDE. However, it should be noted that because estimates of cod abundance were not available, the multispecies data set did not include the period 1956-60 that was a period of

rather violent fluctuations in rock sole catchability (Fig. 7.5).

Tests of the Switching Hypothesis

Switching by fishermen between cod and flatfish is one potential mechanism that could cause type III responses in the Hecate Strait fishery. However, none of the fits of switching curves were significantly nonlinear (r^2 s ranged from 0.05-0.68; Table 8.13). The fit to one data set was significantly nonlinear at $P=0.08$ (cod and rock sole, fully recruited ages from CAGEAN; Fig. 8.19; Table 8.13). Power was low for all data sets (≤ 0.54 ; Table 8.13). I failed to detect any evidence of heteroskedasticity or non normality in the residuals from 10 of the 12 data sets (Table 8.13).

The overall results do not provide evidence for switching. However, as indicated by the low power, variability in data and or small effect sizes resulted in weak tests of the switching null hypothesis in most cases.

Summary of Results

The major results from my investigation of functional responses in Hecate Strait are:

1. A generalized equation capable of mimicking response types I-IV resulted in a type III (sigmoid) functional response for 11 of the 12 data sets.
2. Five comparisons of alternative single species models found statistically significant differences; all five indicated that a sigmoid response was most consistent with the data.
3. In many cases, the best fit disc equation (type II response) was linear, not saturating, and for cases where a saturating response

Table 8.13. Summary of tests of the switching hypothesis. From left to right are the data source (species1 and age range/species 2 and age range), the catch-at-age method, the estimate of alpha, the degrees of freedom (df; $n=df+2$), the estimate of beta and its standard error, the t value and the probability (P) for test of $H_0: \beta \leq 1$, the power to the t-test, and the coefficient of determination (r^2). Also given are for tests the normality of residuals, Stephens' (1974) modified A^2 statistic and corresponding P value, and for tests of homoskedasticity of residuals, Kendall's τ_b and corresponding P value.

Data source	method	alpha	df	Beta	SE(beta)	t	P($\beta \leq 1.0$)	Power	r^2	Normality		Homoskedasticity	
										modified A^2	P	τ_b	P
Cod410/Eng610	CAG	0.76	17	1.11	0.22	0.50	0.31	0.12	0.59	0.32	>0.15	-0.26	>0.12
Cod210/Eng317	CAG	0.87	17	0.99	0.43	-0.01	0.51	0.05	0.24	0.43	>0.15	-0.12	>0.49
Cod410/roc610	CAG	0.86	16	1.34	0.23	1.45	0.08	0.41	0.68	0.21	>0.15	-0.06	>0.77
Cod210/roc415	CAG	0.73	16	1.05	0.39	0.12	0.45	0.06	0.31	0.28	>0.15	-0.14	>0.45
Cod410/Eng610	VPA	0.81	17	0.92	0.20	-0.38	0.65	0.10	0.55	0.31	>0.15	-0.18	>0.30
Cod210/Eng317	VPA	1.29	17	0.43	0.48	-1.19	0.87	0.30	0.05	0.31	>0.15	-0.23	>0.19
Cod410/roc610	VPA	0.97	16	1.30	0.36	0.83	0.21	0.20	0.44	0.73	<0.05	0.19	>0.29
Cod210/roc415	VPA	0.59	16	1.18	0.36	0.50	0.31	0.12	0.40	0.47	>0.15	-0.07	>0.71
Eng610/roc610	CAG	14.01	21	0.57	0.24	-1.81	0.96	0.54	0.21	0.51	>0.15	0.38	<0.01
Eng317/roc415	CAG	0.42	21	0.72	0.51	-0.56	0.71	0.13	0.08	0.26	>0.15	-0.08	>0.64
Eng610/roc610	VPA	13.60	21	0.56	0.31	-1.46	0.91	0.39	0.14	0.65	>0.05	0.20	>0.19
Eng317/roc415	VPA	0.37	21	0.77	0.45	-0.51	0.69	0.13	0.12	0.27	>0.15	-0.08	>0.64

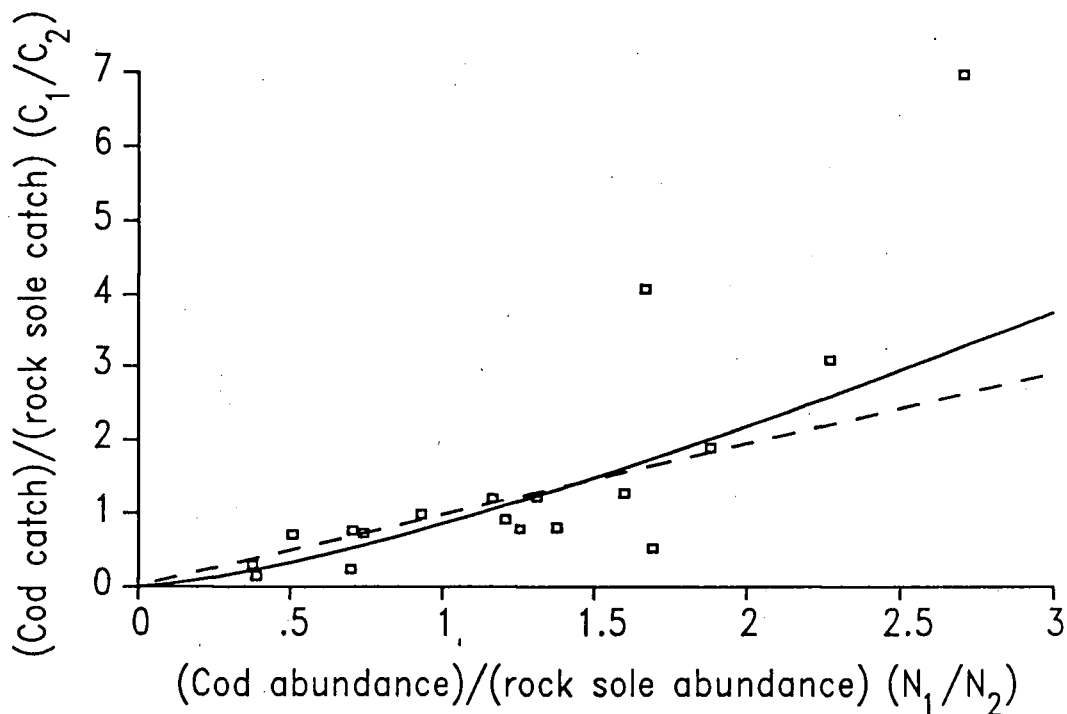


Figure 8.19. Predicted switching curves for data set from CAGEAN for cod and rock sole and fully recruited ages (4-10;6-10). Squares are observations. Dotted line is the line of no preference (i.e. where α and $\beta = 1.0$). Statistics for the fit of the curve are given in Table 8.13.

was indicated, it did not have a statistically better fit than either a linear (type I response) or sigmoid model.

4. The single species mortality models fit most data sets poorly, although in most cases for a given data set and model, the qualitative form of the response was consistent with the corresponding functional response.
5. The statistical power of the tests of alternative single species functional response models and of tests of significance of the slope in the linear single species mortality models was low in all cases where I failed to reject the null hypotheses.

6. Multispecies functional response and mortality models often resulted in better fits than single species models for all species. In some cases, the increase in r^2 s were quite large. However, formal statistical comparisons of multispecies and single species models were not possible because of differences in the data sets used by the two types of models.
7. Switching was not detected in any of the data sets, although power was low in most cases.

Discussion

Outstanding Issues

Statistical Issues

I examined residuals to test for violations of two principal assumptions of my least squares fits (normality and homoskedasticity), however there are other assumptions that were not investigated. Violations of these other assumptions such as (1) measurement errors in abundance estimates (i.e. the X variate; Ludwig and Walters 1981; Walters and Ludwig 1981), (2) autocorrelated residuals (Glasbey 1980), or (3) residuals correlated with subsequent levels of the X variate (i.e. the so called "time series" bias; Walters 1985), or (4) combinations of (1) and (3) above (Caputi 1988) may lead to biased estimates of functional relationships, and/or imprecise parameter estimates.

Abundance estimates from VPA and CAGEAN are certainly imprecise and possibly biased under certain conditions, particularly if input parameters are in

error (reviewed in Ch. 7). Thus, I restricted my statistical comparisons to the functional response models, because the mortality curves are particularly sensitive to measurement errors since errors in abundance affect both variates (Shardlow et al. 1985). For simple linear regression, it is possible for a given set of model parameters and MSE to determine how imprecise the abundance estimates would have to be in order to change particular conclusions regarding the functional relationship (e.g. Shardlow et al. 1985). For nonlinear fits, estimating the effect of measurement error requires extensive Monte Carlo trials, preferably with "fake data" where the correct parameters are known (e.g. Walters and Ludwig 1981). However, Walters and Staley (1987) note that using Monte Carlo simulation to derive correction factors for actual data sets does not always completely correct for the bias. I did not perform such simulations, but drawing analogy from measurement error studies of stock-recruitment relationships, I suspect that measurement errors would cause an overestimate of slope parameters (i.e. the rate of effective search) and an underestimate of asymptote parameters ($1/t_h$; i.e. overestimate of handling time).

I did not examine the residuals from alternative model fits for autocorrelation. For linear regressions, standard corrections are available that generally involve transforming the data (by differencing) to correct for autocorrelation (e.g. Kmenta 1986), and similar procedures are used for nonlinear least squares problems (e.g. Glasbey 1980, Bates and Watts 1988). However, failing to account for autocorrelated deviations does not generally result in biased estimates, but rather incorrect estimates of the precision of parameter estimates (Kmenta 1986). In particular, Glasbey (1980) notes that failing to correct for positively autocorrelated deviations in nonlinear least squares applications may lead to parameter variance estimates that are too small. Thus, correcting for

autocorrelation might have changed the P values and power of the *t*-tests used to test certain parameters (e.g. *b* in the linear single species mortality model, or β in the switching model). However, given that power of these tests was generally very low a P values were generally quite high, precision would have to change substantially in order to affect the results.

My tests for homoskedasticity did not identify many cases where the ranks of the absolute value of residuals were correlated with the ranks of the X variates (i.e. abundances). Furthermore, it is unlikely that deviations in LPE would cause deviations in abundance, except perhaps for long lived stocks subject to severe overexploitation (e.g. through recruitment overfishing). Thus, while the tests for homoskedasticity do not provide the exact evidence necessary to discount a potential time series bias, I suspect that the effect of the time series bias was small in my case.

Finally, as demonstrated by Caputi (1988), effects of combinations of measurement errors and time series biases may interact. Therefore, he suggests that the two sources of error should be evaluated simultaneously through carefully designed simulations in order to determine the overall effect.

In my tests of goodness of fit to alternative functional responses, I assumed that errors were normally distributed. In some cases, particularly for fits to the rock sole data sets, the test for normality showed that there was only a small chance (i.e. $P < 0.01$) that the observed residuals could have been drawn from a normal distribution. Furthermore, other studies (e.g. Bannerot and Austin 1983; Sweirzbinski 1985) suggest that observations of L/E are probably distributed lognormally or as a negative binomial. Thus, assumptions of the least squares techniques may have been met more consistently if I log transformed the

data. Indeed, this possibility was confirmed in my tests of residuals from fits of Fox's (1974) loglinear model (i.e. eq. 6.10 fit by eq. 6.12, Ch. 6; results not reported here), where I found no evidence for non normality for the rock sole data sets, and only one case of significant non normality (for English sole) for the remaining eight data sets. However, the Fox model does not permit comparisons of type III vs. either type I or type II responses.

Biological Issues

My functional response models ignored potential interference effects. There are various mechanisms that could cause interference effects in fisheries (e.g. disinformation). However, I suspect interference effects to be most important over short time scales (i.e. days or possibly weeks) and small spatial scales, not over Hecate Strait as a whole on an annual time scale.

Given the large variability about most of the fitted functional relations, it is worth considering some factors that may have contributed to the variability. Some of the variation in annual LPE may simply be due to individual variation in LPE among vessels (e.g. Hilborn and Ledbetter 1985). However, I suspect that the effect of individual variation should to some extent average out over large spatial and temporal scales (e.g. for years and areas the size of Hecate Strait).

Ironically, the same factors (large spatial and annual temporal scale) that may have reduced the effects of individual variation, may introduce variability from other sources. For example, spatial changes in fleet distribution within Hecate Strait among years would cause variation in LPE and q . Similarly, intra-annual changes in fleet distributions for a given subarea within Hecate

Strait could also cause variability in LPE and q .

Another potential cause of some of the variation may be nonrepeatability perhaps due to nonstationarity of the parameters of the functional relationships. Thus, the parameters of the functional responses may have changed over the time series resulting in different observed LPE or q values for the a given abundance level (Walters 1986, 1987b). Evidence for nonrepeatability is presented in Figure 8.20. Nonrepeatability is most evident in the plots for English sole LPE and q ; note in particular, the difference in the response in the early 1960's compared the rest of the time series (Fig. 8.20). The plots for cod show evidence for nonrepeatability, particularly at low abundance levels.

The plots for rock sole LPE and q appear to show good repeatability with a few outliers (i.e. '58, '61, 67'). Nonrepeatability may have resulted from a variety of factors including incompletely standardized effort data, long term shifts in the distributions of fish, or changes in fleet composition in Hecate Strait due to changes in alternative fishing opportunities. In the case of the English sole, some of the nonrepeatability is probably due to affects of cod abundance. For example, the decrease in English sole LPE and catchability during the early 1960's occurred when English sole abundance was decreasing and cod abundance was increasing (Fig. 8.20; Fig. 7.4, p. 185). Also, fitting a multispecies model that included cod abundance considerably improved the fit of both functional response and mortality curves.

Errors in estimated abundances (discussed above) may also be responsible for some of the observed variability about functional relationships (e.g. q vs abundance; Shardlow et al. 1985).

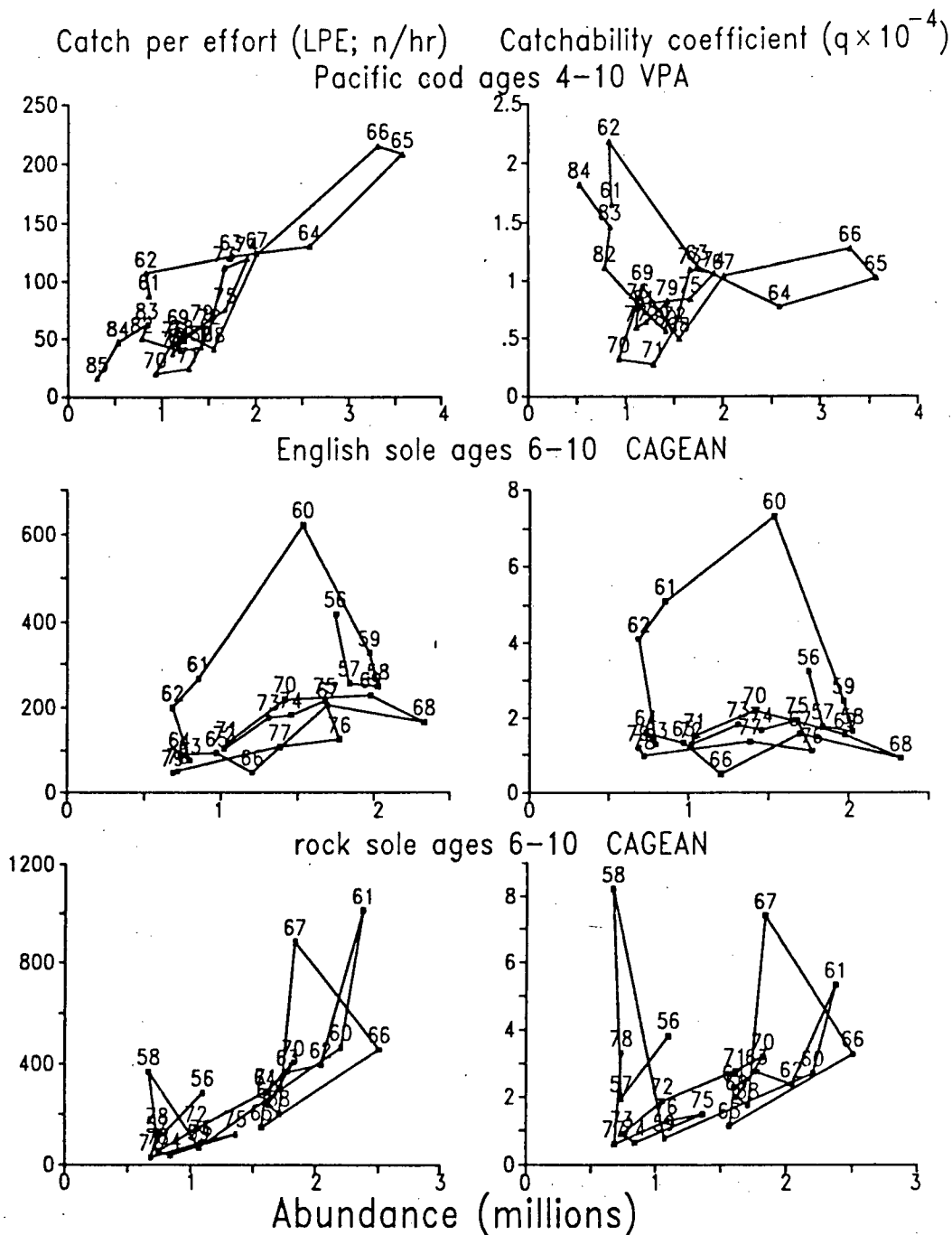


Figure 8.20. Times series plots of LPE and Catchability (q) vs. abundance for selected data sets for each species. Numbers above points denote years, and points for each year are connected sequentially in chronological order. "Loops" of years for LPE and q indicate nonrepeatability in the functional and mortality responses respectively. Data sets used are indicated above each plot.

Both catch-at-age models that I used to reconstruct abundances assumed that natural mortality (M) was constant. However, if M changed over time, or particularly if M was density dependent, apparent relationships between LPE and abundance and q and abundance could be artifacts. Evidence for density dependent M has been found for Pacific cod suggesting that M increases with decreasing abundance (Fournier 1983). If M is depensatory, my estimates of abundance would be underestimates for low abundances and overestimates for high abundances. Thus, had I found evidence for type II responses in cod, it could have been a result of incorrectly assuming a constant M .

However, all type II fits were linear for cod, and the only significant difference found suggests that of the three alternatives the type III response is most evident. If the relationship between M and density was dome shaped, the sigmoid response might be an artifact of using a constant M . However, there is no evidence for a dome shaped M pattern in Pacific cod. Furthermore, there is no evidence that M is density dependent for either of the flatfish species.

One of the most consistent patterns in the results from fitting the functional response models was the lack of consistent statistical evidence for an asymptote in either the single or multispecies fits. In order to understand the potential reasons for this finding, it is necessary to recall the potential mechanisms that lead to saturation in the functional response.

In the case of single species models, the asymptote arises primarily because of the effects of handling time on searching time. However, the effort measure I used, hours trawled, does not include handling time, and it may even be roughly proportional to searching time. Thus, I may have found greater evidence for an asymptote in the functional response had I used a different

effort measure, such as days fished.

In the case of multispecies models, a saturating response could arise through handling time affects as well, but also through the effect on search time of switching to alternative prey. For example, if (1) total foraging time was composed of time spent foraging for two species (s_1 and s_2 ; i.e. $T = T_{s1} + T_{s2}$) and (2) LPE was measured as L/T and (3) fishermen spent more time searching for species 1 as its abundance increased, then the time available for searching for species 2 would decline. Thus a saturating response could arise for species 2, if species 1 was more abundant than species 2, and the two species had similar temporal trends in abundance (e.g. cod and English sole). However, I measured LPE as L/T_{si} , thus reducing my chances of seeing a asymptote in the multispecies responses.

My main reason for choosing hours trawled allotted by species as the effort measure was that it is the effort measure used by fisheries biologist and managers and I wanted to consider the potential implications of functional responses on assessment and management. Some of these implications are presented in the next section.

General Implications

Several studies have reviewed the various consequences of type II functional responses for fisheries (e.g. Ulltang 1980; Peterman and Steer 1981; Crecco and Savoy 1985; reviewed in Ch. 6). I did not find any quantitative evidence for type II responses in the LPE data for the reasons mentioned above. Thus my discussion focuses on two areas; (1) potential implications of type III responses, and (2) the implications of multispecies responses particularly for less

abundant species in a multispecies fishery

Implications of Type III Functional Responses

Most investigations of functional responses in fisheries (reviewed in Ch. 6) have focused on "single" species fisheries, and therefore most studies have not tested for, or considered the possibility of sigmoid functional responses. Of the studies reviewed in Chapter 6, only Peterman (1980) fit an equation that could potentially result in a type III response, but he found parameter conditions consistent with type II response. I found statistical evidence for a type III response for 3 of 12 data sets, however a type III functional responses can be expected for multispecies fisheries particularly if fishermen switch their effort among species. I failed to detect switching in the trawl fishery. However, my tests of the switching hypothesis had low power and given the various mechanisms for switching in fisheries reviewed in Chapter 6, I suspect that multispecies fishermen are switching predators. As noted by Murdoch and Oaten (1975), switching commonly but not always leads to a sigmoid functional response.

Sigmoid functional responses have implications for several aspects of fisheries including: (1) interpretation of abundance indices based on LPE and the potential management response based on such indices, (2) equilibrium yield vs abundance relationships used to determine maximum sustainable catches, and (3) simulation models used to investigate alternative management strategies.

If a manager assumed a linear functional response when the correct response was sigmoid, his LPE indices would overestimate abundance at low stock sizes and underestimate abundance at high stock sizes (e.g. Fig. 8.1 B;

data set from CAGEAN ages 2-10). Thus, the manager might tend to be overly optimistic when abundance was low and overly conservative when abundance was high. Fortunately, the mortality curve would compensate for potential over- or under- harvest, particularly for management tactics base on regulating effort, because the manager would tend to overestimate catchability at low stock sizes and underestimate it at high stock sizes (e.g. Fig. 8.7 B; data set from CAGEAN ages 2-10).

Fisheries yield models that assume logistic growth and a type I mortality curve for fishermen usually predict a dome shaped relationship between yield and population size or yield and effort (Ricker 1975). In the case of type II responses, the dome may be positively skewed or even bend back toward the origin (Fox 1974; Condrey 1984). The domed shape arises because population models that assume logistic growth and density independent mortality (i.e. a type I mortality curve) have two equilibria: zero, and the natural equilibrium corresponding to resource limitation as some life stage (e.g. P_1 , Fig. 8.21A; Peterman et al. 1979).

However, for type III mortality curves two intermediate potential equilibria may be added (Peterman 1977, Peterman et al. 1979), (e.g. Fig. 8.21B). The points P_1 and P_3 are points of attraction (or equilibria) since population sizes above these levels will tend to decrease (since $N_{t+1}/N_t < 1.0$) and populations below these levels will tend to increase. The point P_2 is unstable for the opposite reasons. The area between points P_2 and P_3 is known as a predator pit, because if the population decreases to a level between points P_2 and P_3 , it will tend to remain there until more favorable than average survival or reproductive conditions allow it to escape. Note also that the size of the pit (i.e. the distance between

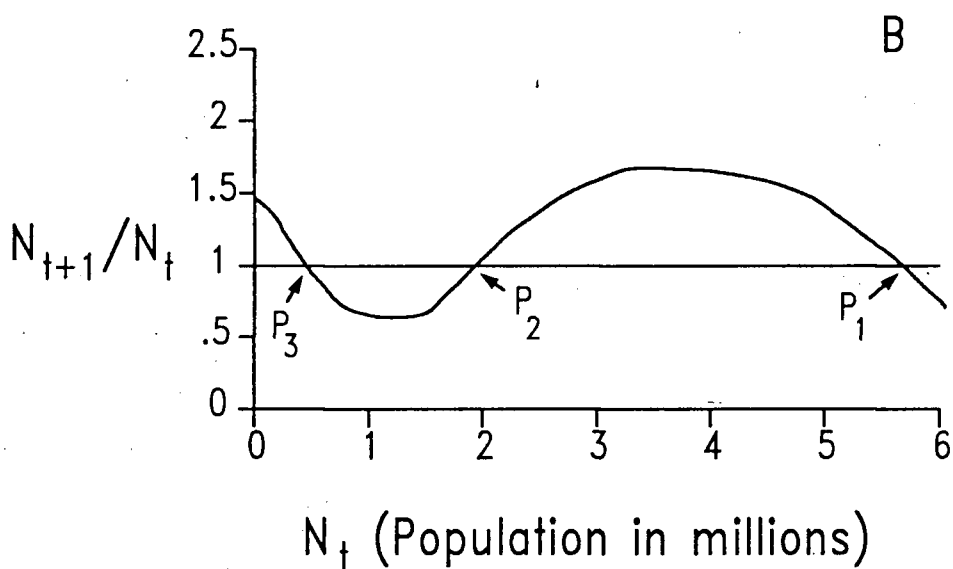
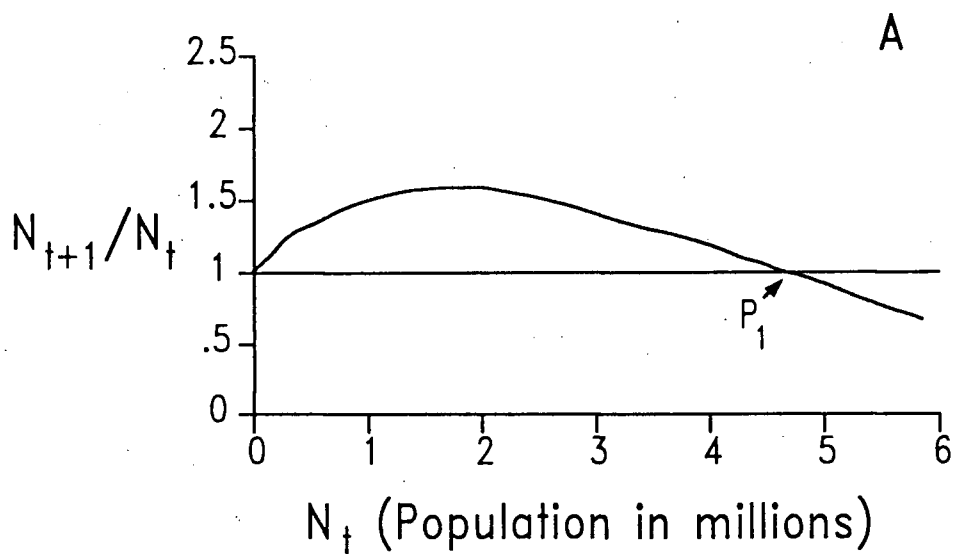


Figure 8.21. Schematic plots population growth rate (N_{t+1}/N_t) vs. population size for two hypothetical fish populations. Population in A has one stable equilibrium point (P_1) caused by limitations at high abundances (space, food). Population in B has in addition to P_1 , a lower stable equilibrium point P_3 and an intermediate unstable equilibrium point, P_2 . The area beneath the 1:1 line between points P_3 and P_2 is called the predator pit and it is caused by compensatory mortality at intermediate N .

P_2 and P_3) can be affected by harvesting because N_{t+1}/N_t is decreased due to the fraction removed by harvesting (Peterman et al. 1979). Thus, the potential for the population to become trapped at low levels increases as harvest rate increases. The potential for a predator pit in fish populations caused by other fish predators was suggested by Peterman (1977), but if fishermen have sigmoid functional responses, they may cause predator pits themselves or act as another component in affecting existing pits caused by other predators.

Type III functional responses also have implications for simulation models of fish populations used to explore alternative harvest strategies. If the true response is type III rather than a type I response (i.e. Baranov Catch equation) there will be a greater likelihood of a stock collapse to some low level at high harvest rates because of the predator pit discussed above. Thus, simulations would underestimate the probability of stock collapse or the probability of no fishing (i.e. proportion of simulations the stock falls below some arbitrary cutoff) if they ignore the response pattern.

One of the barriers to including type III responses in fisheries models is the lack of an appropriate equation. The various equations I presented for a type III response in Chapter 6 were all instantaneous equations, thus they ignore the effects of prey depletion. The derivation of exploitation models for type III responses is difficult and generally the resulting equations are quite complicated (e.g. see exploitation model for the generalized equation; eq. 36, Fujii et al. 1978). Furthermore, the resulting equations commonly involve NA (i.e. Catch) on both sides and thus must be solved iteratively. And finally, even if these problems could be overcome, parameter estimates would have to be determined (i.e. a , t_h , c) using the exploitation model because using estimates from fitting the instantaneous form would tend to overestimate the catch.

However, in cases where both exploitation and instantaneous models have been fit to the same data sets, they each describe the data equally well (e.g. Rogers 1972). Thus, for the purposes of simply investigating the implications of type III responses on hypothetical populations, instantaneous equations are probably adequate (e.g. Peterman 1977).

Implications of Multispecies Functional Responses

A common problem in multispecies fisheries assessment is how to determine effective fishing effort for individual species when they are caught together (e.g. Westrheim 1983). The goal is to find an effort measure that results in a LPE index that is approximately proportional to abundance (or is some function of abundance). The problem is particularly acute for species that are not the major target, but generally are bycatch or are sought after when the major target is in short supply (e.g. Westrheim et al. 1988).

The poor fits of single species functional response models for the flatfish and the considerable improvement of in fit of the MSDE (especially for rock sole) clearly indicate that even LPE indices based on allocated effort may depend to a large degree on the effects of alternative species. Thus, an alternative approach to dividing the effort among species would be to model LPE using the total effort (all species) and a MSDE that explicitly takes account of the effects of abundance of alternative species. It is possible to solve the MSDE for each species for abundance and use the set of three equations to predict abundance given LPE and parameter values (a , b , c , and d) from historical data (Carl Walters, Univ. of British Columbia, Vancouver, BC, pers. comm.).

The potential for predator pits resulting from type III mortality curves has implication for multispecies situations as well (e.g. Peterman 1977). For example, if both the major and minor species have predator pits and the major species has a higher optimum harvest rate, harvesting at a rate appropriate for the major species may force the minor species into its predator pit. The situation could go undetected, particularly if the catch of the minor species is underestimated because of discarding. Thus the detection of type III response may be particularly critical in multispecies situations.

Perspectives for Future Research

This section briefly considers directions for future research in the study of numerical and functional responses in fisheries.

I applied one approach to examining movement patterns, hypothesis testing, and discussed three others, models of fisherman choice, search theory applications, and simulation modelling. Which of these techniques or combinations of techniques will prove valuable in the future depends on the objectives for studying movement patterns. If the objective is to improve the management of fisheries, then further hypothesis testing followed by more detailed simulation modelling may prove most fruitful in the short run because these two approaches are most easily applied to existing data. However, theoretical aspects of movement dynamics would be best advanced by pursuing the application of choice models and search theory, and these approaches may also have long term benefits to management.

One of the problems inhibiting further progress by any of the approaches is the lack of data gathered specifically for the purpose of studying movement patterns. Thus one key to future advances will be to gather the appropriate data to test the hypotheses, to describe the relative benefits of alternative choices, to describe the underlying spatial distributions of fish, and to fit the simulation models. Specifically, data on fishing costs itemized within trips and for smaller areas (e.g. costs for fuel steaming between grounds, searching and trawling on grounds) and daily area-specific LPE data would be particularly valuable for examinations of within trips movement patterns. Given the influx of electronic equipment on modern fishing vessels, one possible way to collect this data would be to use "on board" computers.

Understanding movement patterns requires an interdisciplinary approach, but unfortunately various disciplines have generally followed separate paths; mathematicians have focused on search theory applications, economists have pursued choice models, and biologists have tested hypotheses and built simulation models. One of the challenges ahead will be to get these disciplines to work together, perhaps by focusing attention on a simulation model of a particularly data rich fishery.

It is likely that fisheries scientist and managers will continue to rely on landings per unit of fishing effort as an index of the abundance of fish (at least for short term predictions). Thus, the importance of understanding functional responses in the fishery is unlikely to diminish. The fundamental issues are the choice of effort measure for use in the desired functional response model and how to include the affects of alternative prey in multispecies fisheries.

Most functional response models assume random search by the predator and predict that catch per unit of time spent searching is proportional to abundance. Thus if managers want to continue to used linear functional response models, catch per unit of search time would be the ideal index. Unfortunately, fishermen probably do not search randomly, at least not on the large spatial scales commonly used for management, and even if they did, obtaining accurate estimates of search time could be difficult.

Yet if my analysis of the British Columbia trawl fishery is at all representative, assuming landings per hours trawling (the common index used in trawl fisheries) is proportional to abundance can be misleading. While fisheries scientists have certainly recognized the potential pitfalls of this assumption, there is still further research needed. I believe that detailed time budget analyses of

the fishing process is the next essential step toward improving the accuracy of abundance indices. Time budgets studies could easily provide estimates of handling time and, if combined with spatial mapping of the fish abundance, might even provide estimates of the rate of effective search (α ; proportion of area search by one unit of fishing effort). These two parameters could be used to correct LPE indices that use aggregate effort measures such as days fished for saturation effects. Repeated measure of the rate of effective search at different abundance levels be used to develop sigmoid response models. Application of functional response models that assume non random search (e.g. Fujii et al. 1978; Mace 1983) or two stage models (i.e. non random search for patches, but random exploitation within a patch; Griffiths and Holling 1969) would also improve future studies of functional responses in fisheries.

The application of multispecies functional responses may be a valid alternative to methods that attempt to allot effort to individual species in multispecies fisheries. Specifically, the multispecies disc equation can be rearranged to solve for N in terms of LPE for each species and the resulting set of equations (1 for each species) can be used to correct LPE indices of a given species for the effects of the abundance of alternative species. But further research is needed, particularly in developing models to predict discarding of bycatch species.

Finally, effective examination of movements patterns or functional responses requires the cooperation of fishermen. Obtaining cooperation can be difficult, especially in situations where adversarial relationships between fishermen and management have existed for long periods. It is unlikely that this cooperation will be attained through broad changes in the philosophy or approach of government agencies, but rather through the success of a few individuals gaining

cooperation on a one to one basis.

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Appendix A

Table A1. Estimated numbers landed-at-age ($\times 10^3$) of Pacific cod from Hecate Strait (Areas 5C+5D) for 1961-85.

Year	Age								
	2	3	4	5	6	7	8	9	10
1961	58	369	160	31	5	3	3	0	0
1962	165	223	132	65	26	8	2	2	0
1963	342	543	260	77	17	12	5	1	0
1964	1358	668	279	108	21	4	1	1	0
1965	314	2162	912	197	51	4	4	0	0
1966	384	1554	1043	305	76	10	1	1	0
1967	889	591	339	148	58	18	5	1	0
1968	113	1322	334	150	72	20	6	3	0
1969	314	185	375	96	27	13	2	1	1
1970	84	313	86	16	11	4	1	0	1
1971	379	138	94	44	6	4	3	0	0
1972	908	288	155	49	7	7	1	4	0
1973	695	811	277	66	37	6	2	2	1
1974	1158	465	372	122	32	5	3	2	0
1975	591	926	364	187	22	37	14	7	0
1976	498	1125	308	110	43	20	2	3	0
1977	935	543	272	50	32	10	0	0	0
1978	79	449	213	62	9	7	2	0	0
1979	1349	345	452	106	33	6	3	0	1
1980	676	934	384	96	34	12	2	1	0
1981	407	438	436	154	22	14	0	0	0
1982	222	382	172	54	15	3	1	1	0
1983	225	432	258	88	21	6	1	0	0
1984	348	247	174	54	19	1	2	0	0
1985	75	237	73	24	13	2	1	0	0

Table A2. Estimated numbers landed-at-age ($\times 10^3$) of female English sole from northern Hecate Strait (Area 5D) for 1956-79.

Year	Age														
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1956	16	211	600	310	156	85	34	12	12	10	6	0	0	0	0
1957	12	169	140	243	123	56	24	22	12	0	0	0	0	0	0
1958	6	113	252	212	217	100	52	35	11	3	0	3	0	0	0
1959	8	243	436	335	206	130	68	31	21	6	0	2	0	0	0
1960	37	355	488	363	231	257	82	31	16	10	2	4	0	0	0
1961	2	267	645	307	137	68	40	19	12	4	4	0	0	0	0
1962	5	129	292	152	89	28	11	11	4	0	0	0	0	0	0
1963	8	92	175	204	69	29	8	6	0	2	0	0	0	0	0
1964	16	211	270	127	63	28	5	5	1	1	0	0	0	0	0
1965	1	93	233	177	97	45	20	11	2	2	0	1	0	0	0
1966	2	78	190	171	89	38	15	7	0	1	1	0	0	0	0
1967	2	54	388	302	118	54	23	8	5	1	0	0	0	0	0
1968	9	26	161	454	214	90	33	2	2	0	0	0	0	0	0
1969	28	70	107	194	358	132	43	15	0	2	1	0	0	0	0
1970	47	215	145	116	184	213	71	25	4	0	2	0	0	0	0
1971	31	250	136	49	50	55	66	25	8	3	0	0	0	0	0
1972	15	90	155	121	78	43	20	8	3	2	1	1	0	0	0
1973	145	183	221	101	44	34	32	16	10	0	0	0	0	0	0
1974	60	172	153	107	76	33	22	10	3	12	3	10	9	0	1
1975	35	273	381	281	199	101	60	15	3	7	4	2	2	0	0
1976	13	132	382	310	205	103	59	12	3	6	4	4	4	1	0
1977	92	238	325	232	147	66	37	13	2	4	2	5	2	1	6
1978	27	79	121	73	52	43	30	8	1	0	2	0	0	0	0
1979	105	200	219	135	98	71	47	14	2	3	2	2	2	0	0

Table A3. Estimated numbers landed-at-age ($\times 10^3$) of female rock sole from northern Hecate Strait (Area 5D) for 1956-78.

Year	Age											
	4	5	6	7	8	9	10	11	12	13	14	15
1956	58	78	164	148	89	49	16	5	4	1	1	0
1957	47	43	87	88	67	36	21	9	2	0	0	0
1958	45	742	148	69	34	40	10	9	2	2	0	0
1959	2	133	101	15	3	2	0	0	0	0	0	0
1960	9	332	508	92	23	8	3	2	3	1	0	0
1961	0	45	498	361	66	5	5	0	0	0	2	0
1962	0	6	91	299	124	23	10	1	0	0	0	0
1963	29	62	98	228	205	78	24	4	5	0	0	0
1964	105	116	60	89	106	44	11	6	1	0	0	0
1965	35	102	101	65	33	17	7	4	2	1	0	0
1966	75	729	661	303	197	121	75	46	18	2	2	0
1967	39	414	354	354	116	53	19	12	2	0	0	0
1968	205	392	671	216	55	24	12	4	0	0	0	0
1969	440	362	245	138	29	11	5	0	0	0	0	0
1970	9	116	247	262	79	82	24	21	2	4	0	0
1971	21	228	365	181	154	74	18	3	0	0	0	0
1972	39	114	114	72	37	19	8	4	2	1	0	0
1973	48	30	20	26	22	13	7	7	4	0	0	0
1974	153	182	14	3	0	6	6	3	0	0	0	0
1975	23	72	222	227	168	96	41	13	5	3	8	3
1976	94	153	266	75	28	13	0	0	0	0	0	0
1977	83	166	112	80	19	8	4	3	2	0	0	0
1978	124	109	81	72	52	34	32	14	11	10	3	1

Table A4. Fishing effort (hours trawled) for Pacific cod (areas 5C+5D), English sole (area 5D), and rock sole (area 5D). Source: Tyler et al. (1985).

Year	Pacific cod	Species	rock sole
		English sole	
1956	--	1300	1538
1957	--	1653	2631
1958	--	2332	742
1959	--	2468	1099
1960	--	1505	989
1961	2312	1676	402
1962	2195	1232	754
1963	3075	3101	1287
1964	3176	2308	1102
1965	5608	3491	1255
1966	6685	5141	3244
1967	4597	2077	918
1968	14190	3144	3337
1969	9049	2571	2122
1970	5925	2402	1672
1971	6142	2708	2466
1972	3910	2211	2268
1973	3502	2265	2568
1974	4477	2318	2212
1975	8373	3415	5864
1976	10582	6757	5609
1977	9841	7594	8085
1978	6146	4714	3453
1979	9863	8651	--
1980	12304	--	--
1981	15598	--	--
1982	4933	--	--
1983	6038	--	--
1984	5329	--	--
1985	7161	--	--

Table A5. Age specific net fecundities, e_a (eggs), used in CAGEAN for Pacific cod, English sole and rock sole.

Age	Species		
	Pacific cod ¹	English sole ²	rock sole ²
2	120,588	--	--
3	783,921	45,000	--
4	1,510,883	250,000	125,000
5	2,192,303	595,000	245,000
6	2,849,446	1,080,000	585,000
7	3,447,840	1,500,000	850,000
8	3,957,208	1,700,000	950,000
9	--	1,850,000	1,100,000
10	--	1,950,000	1,200,000
11	--	2,050,000	1,300,000

1 Source: Ketchen (1961,1964), Thomson (1962)

2 Source: J. Fargo, Pacific Biological Station, Nanaimo, B.C.

Table A6. "Best" estimates of starting parameter values used in VPA and CAGEAN for Pacific cod, English sole, and rock sole.

Species	Parameters					
	M_B	$q_B(X10^{-5})$	E_t (hours trawled)	$F_B=q_B E_t$	λ_1	λ_2
<i>Pacific cod</i>	.68	5.79	7161	.41	.5	.5
<i>English sole</i>	.22	4.09	8651	.35	.5	.5
<i>rock sole</i>	.25	5.17	3453	.18	.5	.5

Table A7. Starting input parameters generated by CAGEAN's routine COHORT given best estimates of starting parameter values (see Table A6) for Pacific cod, English sole, and rock sole. $P_{a,t}$ denotes population numbers ($\times 10^3$) of age a fish in year t . F_t denotes fishing mortality in year t . S_a denotes the selectivity of age a fish. q is the catchability coefficient, and a and b are spawner-recruit parameters.

number	Pacific cod		Species English sole Parameters		rock sole	
	name	value	name	value	name	value
1	P8-10,61	11	P11-17,56	105	P11-15,56	75
2	P7,61	35	P10,56	69	P10,56	123
3	P6,61	121	P9,56	167	P9,56	233
4	P5,61	211	P8,56	399	P8,56	186
5	P4,61	734	P7,56	689	P7,56	454
6	P3,61	1736	P6,56	1135	P6,56	439
7	P2,61	5487	P5,56	2005	P5,56	426
8	P2,62	8964	P4,56	2149	P4,56	936
9	P2,63	12297	P3,56	2406	P4,57	2234
10	P2,64	16579	P3,57	2341	P4,58	3042
11	P2,65	8911	P3,58	2312	P4,59	5649
12	P2,66	6039	P3,59	2479	P4,60	2118
13	P2,67	7983	P3,60	1828	P4,61	1240
14	P2,68	2800	P3,61	1320	P4,62	1276
15	P2,69	7109	P3,62	1751	P4,63	2618
16	P2,70	4729	P3,63	2244	P4,64	2804
17	P2,71	5199	P3,64	2705	P4,65	3060
18	P2,72	8618	P3,65	3976	P4,66	3321
19	P2,73	6690	P3,66	2450	P4,67	2404
20	P2,74	7098	P3,67	1353	P4,68	3070
21	P2,75	7035	P3,68	1460	P4,69	1861
22	P2,76	5762	P3,69	1871	P4,70	1202
23	P2,77	6528	P3,70	1810	P4,71	2357
24	P2,78	5380	P3,71	2091	P4,72	1757
25	P2,79	7699	P3,72	2287	P4,73	1784
26	P2,80	4351	P3,73	2930	P4,74	1933
27	P2,81	4062	P3,74	2549	P4,75	1500
28	P2,82	2977	P3,75	1829	P4,76	1261
29	P2,83	1982	P3,76	1534	P4,77	1489
30	P2,84	2923	P3,77	1846	P4,78	2404
31	P2,85	756	P3,78	1754	F56	.44
32	F61	.24	P3,79	1394	F57	.55
33	F62	.38	F56	.28	F58	.68
34	F63	.52	F57	.22	F59	.09
35	F64	.34	F58	.31	F60	.28
36	F65	.44	F59	.43	F61	.34
37	F66	.57	F60	.92	F62	.22

38	F67	.46	F61	.89	F63	.36
39	F68	.69	F62	.58	F64	.18
40	F69	.64	F63	.46	F65	.09
41	F70	.24	F64	.31	F66	.75
42	F71	.21	F65	.60	F67	.67
43	F72	.22	F66	.40	F68	.53
44	F73	.29	F67	.51	F69	.18
45	F74	.36	F68	.38	F70	.49
46	F75	.60	F69	.45	F71	.60
47	F76	.80	F70	.53	F72	.25
48	F77	.52	F71	.37	F73	.13
49	F78	.33	F72	.19	F74	.03
50	F79	.56	F73	.17	F75	.78
51	F80	.71	F74	.16	F76	.14
52	F81	.80	F75	.42	F77	.10
53	F82	.45	F76	.57	F78	.18
54	F83	.71	F77	.49	S4	.35
55	F84	.65	F78	.22	S5	.80
56	F85	.43	F79	.35	S11-15	1.04
57	S2	.28	S3	.05	q	1.45E-04
58	S3	.74	S4	.31	a	9.12E-04
59	q	7.11E-05	S5	.73	b	1.93E-22
60	a	9.12E-04	S11-17	1.02		
61	b	1.93E-22	q	1.32E-04		
62			a	9.12E-04		
63			b	1.93E-22		

Table A8. Numbers-at-age ($\times 10^3$) of Pacific cod in Hecate Strait (Areas 5C+5D) for 1961-85 estimated from VPA using best estimates of input parameters; $M_B=0.68$ and $q_B=5.79 \times 10^{-5}$.

Year	2	3	4	Age 5	6	7	8	9	10
1961	6518	1561	588	187	59	17	9	0	0
1962	9441	3243	535	188	73	26	6	3	0
1963	12357	4642	1480	180	51	20	8	2	0
1964	16671	5988	1965	568	39	14	0	0	0
1965	9662	7460	2556	797	213	6	6	0	0
1966	5747	4650	2294	676	268	72	0	0	0
1967	7769	2629	1296	465	139	84	29	0	0
1968	3352	3301	922	422	135	32	30	12	0
1969	4837	1610	781	240	112	21	3	11	3
1970	4291	2219	684	147	57	38	2	0	5
1971	5474	2104	903	285	63	21	17	0	0
1972	8705	2496	965	390	114	28	8	6	0
1973	6397	3759	1060	380	162	52	9	3	0
1974	6824	2744	1340	346	147	57	22	3	0
1975	7219	2644	1064	423	93	52	26	10	0
1976	5682	3229	710	290	89	32	3	3	0
1977	6508	2519	870	153	73	17	0	0	0
1978	5356	2636	898	254	43	16	3	0	0
1979	7615	2644	1020	307	86	16	4	0	0
1980	4423	2912	1094	215	84	22	3	0	0
1981	3994	1764	838	293	44	19	3	0	0
1982	2840	1732	591	137	47	8	1	1	0
1983	1772	1277	612	182	33	13	2	0	0
1984	2362	738	353	136	33	3	3	0	0
1985	759	951	206	63	33	4	1	0	0

Table A9. Numbers-at-age ($\times 10^3$) of female English sole in northern Hecate Strait (Area 5D) for 1956-79 estimated from VPA using best estimates of input parameters; $M_B=0.22$ and $q_B=4.09 \times 10^{-5}$.

Year	Age															
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	
1956	2339	2095	1963	955	452	267	103	45	16	16	7	0	0	0	0	
1957	2217	1863	1492	1042	491	225	138	53	26	3	4	0	0	0	0	
1958	2246	1768	1344	1072	620	285	131	90	23	10	2	3	0	0	0	
1959	2356	1797	1318	855	672	305	140	60	41	9	5	2	0	0	0	
1960	2011	1883	1226	670	389	356	130	52	20	14	2	4	0	0	0	
1961	1245	1580	1195	552	219	109	62	32	14	3	3	0	0	0	0	
1962	1806	998	1031	391	173	56	28	14	9	0	0	0	0	0	0	
1963	2781	1444	686	568	179	60	20	13	2	3	0	0	0	0	0	
1964	2714	2225	1077	395	275	83	22	9	5	2	1	0	0	0	0	
1965	4009	2163	1598	624	204	165	42	13	3	3	0	1	0	0	0	
1966	1771	3216	1652	1075	343	79	92	16	1	1	1	0	0	0	0	
1967	1084	1420	2512	1157	711	197	29	60	7	1	0	0	0	0	0	
1968	1087	868	1091	1670	660	466	110	4	41	1	0	0	0	0	0	
1969	1453	864	672	732	937	340	293	59	1	31	1	0	0	0	0	
1970	1763	1140	631	444	415	435	156	197	35	1	23	0	0	0	0	
1971	1837	1373	723	377	254	171	161	63	136	24	1	17	0	0	0	
1972	2092	1446	879	459	259	159	89	71	28	102	17	1	13	0	0	
1973	2453	1665	1081	568	261	138	89	53	49	20	80	13	0	10	0	
1974	1979	1839	1173	671	365	170	81	43	29	30	16	64	11	0	8	
1975	1214	1535	1322	805	443	226	107	45	26	21	14	10	43	0	0	
1976	883	944	989	723	397	180	92	34	23	18	11	7	6	32	0	
1977	702	697	640	455	306	139	54	23	17	15	9	5	3	1	24	
1978	703	481	349	227	161	116	53	11	7	12	8	5	0	0	0	
1979	3292	540	316	173	118	83	55	16	2	4	9	5	4	0	0	

Table A10. Numbers-at-age ($\times 10^3$) of female rock sole in northern Hecate Strait (Area 5D) for 1956-78 estimated from VPA using best estimates of input parameters; $M_B=0.25$ and $q_B=5.17 \times 10^{-5}$.

Year	Age											
	4	5	6	7	8	9	10	11	12	13	14	15
1956	649	434	384	340	177	111	35	13	5	1	1	0
1957	2004	455	270	156	136	61	44	13	5	0	0	0
1958	2941	1520	316	134	46	48	17	16	3	3	0	0
1959	3255	2250	541	118	45	7	3	4	5	0	0	0
1960	1603	2533	1636	333	78	32	3	2	3	4	0	0
1961	1130	1240	1681	831	178	40	17	0	0	0	2	0
1962	1230	880	926	874	334	81	27	9	0	0	0	0
1963	1704	958	679	641	421	152	43	12	6	0	0	0
1964	2862	1301	691	443	301	150	51	13	6	1	0	0
1965	2924	2136	912	486	267	142	78	30	5	4	0	0
1966	2879	2246	1574	621	322	179	96	54	20	3	3	0
1967	2500	2178	1114	651	221	82	36	12	3	0	0	0
1968	2141	1912	1333	558	201	72	18	12	0	0	0	0
1969	1997	1487	1146	457	247	108	36	3	5	0	0	0
1970	1115	1170	842	677	236	166	75	23	3	4	0	0
1971	918	860	809	440	299	115	58	37	1	1	0	0
1972	979	697	470	315	186	100	26	30	26	1	0	0
1973	1111	728	443	267	182	113	61	13	20	19	0	0
1974	1144	823	540	327	185	122	77	41	4	12	15	0
1975	668	756	482	408	252	144	90	54	30	3	9	11
1976	571	500	526	182	122	52	30	34	31	18	0	0
1977	460	363	255	179	77	70	30	23	27	24	14	0
1978	1559	286	138	101	70	44	47	20	16	19	19	11

Table A11. Numbers-at-age ($\times 10^3$) of Pacific cod in Hecate Strait (Areas 5C+5D) for 1961-85 estimated from CAGEAN using best estimates of input parameters; $M_B=0.68$ and $F_B=0.41$.

Year	Age						
	2	3	4	5	6	7	8-10
1961	4670	1530	557	225	60	26	21
1962	7865	2272	674	227	92	24	19
1963	10045	3748	933	247	83	34	16
1964	15055	4686	1431	305	81	27	16
1965	8139	7177	1926	525	112	30	16
1966	6236	3758	2644	596	162	35	14
1967	5712	2811	1275	720	162	44	13
1968	2602	2587	969	356	201	45	16
1969	4259	1133	780	220	81	46	14
1970	4143	1928	390	217	61	22	17
1971	5942	2008	839	156	87	24	16
1972	9176	2877	871	334	62	35	16
1973	7924	4389	1196	325	125	23	19
1974	6557	3716	1706	402	109	42	14
1975	7236	3063	1426	562	132	36	18
1976	6069	3154	926	325	128	30	12
1977	6068	2648	958	212	75	29	10
1978	5293	2734	898	260	58	20	11
1979	6463	2529	1133	333	97	21	11
1980	5161	2902	846	302	89	26	9
1981	4915	2265	898	200	71	21	8
1982	4031	2101	640	184	41	15	6
1983	3415	1866	781	201	58	13	6
1984	6198	1541	636	214	55	16	5
1985	3696	2912	603	216	73	19	7

Table A12. Numbers-at-age ($\times 10^3$) of female English sole in northern Hecate Strait (Area 5D) for 1956-79 estimated from CAGEAN using best estimates of input parameters; $M_B=0.22$ and $F_B=0.35$.

Year	Age								
	3	4	5	6	7	8	9	10	11-17
1956	2397	1994	1512	804	480	271	154	39	288
1957	2176	1906	1450	937	424	253	143	81	231
1958	2035	1736	1428	971	561	254	152	86	223
1959	1745	1620	1273	906	532	307	139	83	211
1960	1568	1383	1128	705	398	234	135	61	185
1961	888	1230	857	459	188	106	62	36	133
1962	1551	700	808	406	157	64	36	21	101
1963	2060	1231	499	475	197	76	31	18	82
1964	2461	1639	899	313	255	106	41	17	70
1965	3484	1960	1206	574	173	141	59	23	61
1966	1483	2769	1410	726	289	87	71	30	56
1967	1016	1184	2092	966	451	180	54	44	61
1968	1212	810	880	1372	559	261	104	31	71
1969	1453	967	608	592	827	337	157	63	72
1970	1959	1156	707	382	319	446	182	85	87
1971	2115	1554	820	410	181	151	211	86	102
1972	2463	1683	1133	511	218	96	80	112	121
1973	3507	1965	1263	762	308	132	58	49	159
1974	2635	2790	1431	786	405	164	70	31	142
1975	1494	2097	2043	904	427	220	89	38	121
1976	1113	1182	1441	1091	375	177	91	37	100
1977	1683	879	795	728	413	142	67	35	82
1978	1927	1321	553	336	207	117	40	19	62
1979	3760	1531	951	334	170	104	59	20	55

Table A13. Numbers-at-age ($\times 10^3$) of female rock sole in northern Hecate Strait (Area 5D) for 1956-78 estimated from CAGEAN using best estimates of input parameters; $M_B=0.25$ and $F_B=0.18$.

Year	Age							
	4	5	6	7	8	9	10	11-15
1956	746	462	364	364	190	132	45	81
1957	1783	551	283	157	157	82	57	71
1958	2632	1327	348	132	74	74	39	74
1959	1998	1942	803	147	56	31	31	63
1960	1040	1545	1460	574	105	40	22	70
1961	851	791	1077	870	342	63	24	63
1962	1364	650	564	677	547	215	39	61
1963	1349	1046	471	367	441	356	140	71
1964	2773	1018	704	257	201	241	195	126
1965	3062	2112	715	426	156	122	146	208
1966	2388	2354	1550	482	288	105	82	253
1967	1983	1692	1182	417	130	77	28	161
1968	2084	1453	995	466	164	51	30	112
1969	1696	1541	891	434	203	72	22	85
1970	999	1272	1007	454	221	104	36	69
1971	478	742	794	459	207	101	47	62
1972	759	350	436	312	181	81	40	57
1973	1487	569	229	222	159	92	41	59
1974	1584	1134	403	142	138	99	57	68
1975	671	1218	833	272	96	93	67	89
1976	899	484	663	272	89	31	30	74
1977	980	657	281	252	104	34	12	57
1978	1325	731	418	134	121	49	16	44