

Trophic and Life History Considerations with Respect
to Multispecies Management Policies

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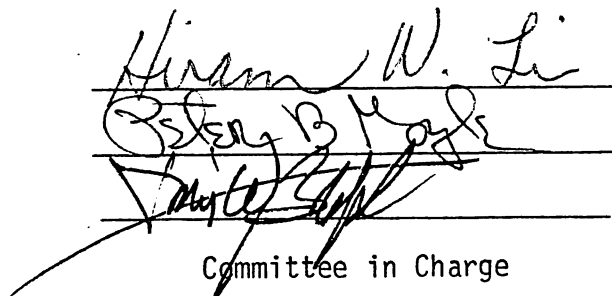
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ABSTRACT

As fisheries become more heavily exploited, the need for multispecies management has become more apparent and trophic relationships are cited as the primary cause for this need for multispecies management. This thesis investigates one aspect of the impact of trophic relationships on multispecies management; indirect effects on food chains by predators. The approach chosen to investigate the impact of trophic relationships on multispecies harvesting is a simulation one. Although the results of a simulation approach are not as powerful as those from an experimental study, the practicality in terms of testing alternative management plans is much higher. The model is of the Catalina nearshore benthic fish community. The choice is a practical one. The feeding habitats of the Catalina nearshore benthic fishes have been studied extensively and a data base of this quality and breadth is necessary for the parameter estimation for this modeling effort. This thesis is divided into four parts: 1) the analysis of feeding selectivity, 2) a review of feeding of benthic fishes at Catalina Island, 3) the modeling effort itself, 4) a review of population parameters and life history patterns of marine fishes.

The first section is a review of feeding selectivity and the development of a selectivity index to measure this selectivity. It is important to distinguish between selectivity and preference. Selectivity is the probability of a predator taking a prey while preference is an innate quality of the organism

which measures absolute desirability. Many factors (availability, learning, predator avoidance, etc.) combine with preference to create selectivity. The currently used selectivity indices have the problem that they change values when a predator feeds with the same selectivity in different prey environments and therefore are unacceptable for use here. A new index is developed for use in the feeding model which does not have this problem.

The focus of this modeling study is the fish which feed on the benthos in nearshore habitats at Catalina Island. The second section is a detailed review of these fish's feeding dynamics and selectivity. This provides the reader with the necessary background to understand the model. This section illustrates some of the inherent problems involved in translating the model structure into a representation of a community.

Models of the benthic feeding fish community were constructed using both a stochastic and a deterministic feeding model. To these models, a harvesting component was added and a multispecies harvesting regime was developed. The multispecies harvesting regime only increased management goals 15 to 26%. The mechanism through which these multispecies management regimes operated were changes in consumption of certain key prey. The population dynamics of these key prey was the most sensitive part of the model and an understanding of the ecology of these key prey may provide a "quick and dirty" approach to multispecies harvesting. The model results were contradictory when compared to the Niche Compression Hypothesis suggesting that this

hypothesis is only appropriate under extremely straightforward feeding conditions.

Population dynamics and life history patterns of marine fishes were examined both to provide the basis for estimates of model parameters and to provide management advice based on these patterns. Life history characteristics varied in consistent patterns and these patterns matched the predictions of r and K selection. The effects of harvesting on stocks with these life history patterns were investigated.

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INTRODUCTION

Historically, fisheries have been managed on a single-species basis assuming that the target species is independent of other species in the community. Usually multispecies fisheries evolve from a situation where one species predominates in value and provides the incentive for development of the fishery. Following this initial phase, a natural succession to a multispecies fishery occurs in which stocks are successively fished down, more fishermen enter the fishery and the relative economic value of other species increases. However, even in these multispecies fisheries, a single-species management regime is retained. Even though it is apparent that these interactions between species should be included in management (FAO 1978; Gulland 1978; Rothschild and Forney 1979), it is not immediately obvious how to do so.

An effective single-species management approach can be justified from either of two assumptions. The first is that the target species are truly independent of all other species in the community and, therefore, have no interaction with any other species. The second is that interspecific interactions of the target species are so weak in comparison with the intraspecific interactions that they can be considered insignificant. The result of either of these assumptions is that interspecific interactions can be ignored. Not until recently have interspecific relations been seriously considered as part of a management plan or as a causal mechanism for fisheries that have collapsed.

The objectives of this thesis are to examine community trophic dynamics, and the influence of trophic structure on management strategies. Although it is realized that other factors (spatial patterns, life history characteristics, environmental forces, etc.) are going to have major effects on interspecific relationships, it is felt that trophic factors will typically be the crucial ones (Moermond 1979).

The approach chosen here is a simulation one. Although the results of a simulation approach are not as powerful as those from an experimental study, the practicality in terms of testing alternative management plans is much higher. In fact, the difficulty of an experimental approach is presumably the reason for the total lack of work in this area. Modeling approaches to problems of large-scale, offshore multispecies fisheries have been attempted before (Larkin 1963, 1966; Pope 1976; Anderson and Ursin 1977; Walter 1979; Knechtel and Bledsoe 1981; Laevastu and Larkin 1981), but they have all had the same difficulty; the parameters are either extremely difficult or impossible to estimate. This leaves these modeling approaches open to serious challenge in their application. In order to avoid these problems, this model will be of the Catalina nearshore benthic fish community. The choice is a practical one. The feeding habitats of the Catalina nearshore benthic fishes have been studied extensively (Hobson and Chess 1976; Hobson et al 1981, in prep.) and, because of this, the trophic dynamics of this community are probably better understood than any offshore community. A data base of this quality and breadth is necessary

for the parameter estimation for this modeling effort. The accumulation of data for a complete description of the trophic dynamics of any community is nearly impossible, but the data are sufficient to allow "intelligent guesses" to be made about those aspects of trophic dynamics not directly investigated.

This thesis is divided into four parts. The first is a review of feeding selectivity and the development of a selectivity index. The underlying logic of the selectivity index overlaps into the model structure, and the selectivity values are central to the modeling effort. The second section is a review of fish feeding at Catalina. This is included to support the model and to provide necessary background. The third part of the thesis is the modeling effort itself. The model will define the major features of the trophic dynamics of the community. To this, a harvest component will be added. The results of the modeling effort provide the basis for generalizations about harvesting multispecies communities. The fourth and final section is a review of life history patterns in marine fishes. This is both to support the estimate of population parameters used in the model and to investigate the implications of these patterns for management directly.

THE ANALYSIS OF FEEDING SELECTIVITY

Introduction

In feeding studies, the relative proportions of prey species in the predator's stomach are commonly found to be different from their proportions in the prey environment. Some prey species occur in stomachs in greater proportion than in the environment, some in less. Differences in the relative composition of stomach contents and environmental densities are the result of feeding selectivity. This concept of feeding selectivity is the focal point of predator-prey dynamics and of optimal foraging, the body of theory dealing with these dynamics.

Feeding selectivity, and its analysis, is important because of the assumption of its adaptive significance. Any dietary analysis, along with the theory on optimal foraging, makes the fundamental assumption either directly or indirectly that a species' goal in feeding is to maximize its net intake of energy subject to other constraints (i.e. exposure to predation, reproduction requirements, etc) (Pyke et al. 1977). The corollary to this assumption is that by maximizing its energy intake, a species would be increasing its reproductive success. The fact that a such a critical assumption would be accepted so universally without substantiation is in itself a strong support for that assumption. Two recent experimental studies, however, have dealt with this directly. The first is a study of the protozoa, Stentor coruleus, feeding on paired combinations of four prey species-- two algal and two nonalgal (Rapport 1980). S

coruleus consistently preferred nonalgal to algal prey, but was indifferent in choosing among alternative algal or alternative nonalgal species. In those cases in which S. coruleus was indifferent to alternative prey combinations, it reproduced equally well on either prey type alone or on combinations of prey types. However, in the cases in which S. coruleus selected a particular combination of prey types in a nonrandom fashion, it reproduced better on a mixture of selected prey than on either prey type alone. The second experiment is with the spider predator, Pardosa vancouveri, feeding on insect larvae (Holmberg 1978). When the spiders were fed preferred prey types, their size and weight were significantly greater than achieved on alternative prey species. In those cases where the spiders were indifferent to two prey types, there were no significant differences in size and weight. The results of these two studies show that food selectivity is high adaptive, enabling species to increase their growth and reproductive rates by exploiting an array of food resources in the most efficient manner.

A great deal of confusion has resulted from not recognizing the difference between the two related concepts of preference and selectivity. Preference is the innate quality of an organism which leads to an ordered ranking of the absolute desirability of a number of different types of prey items. Selectivity is the probability of a prey being eaten by a predator, independent of the abundances of the prey, and is different from preference in that all the complicating factors (such as learning, predator avoidance, etc.) are included. The concepts of preference and selectivity are similar but not identical to Ivlev's (1961)

concepts of predilection and electivity. The failure to recognize the difference between these two distinct, if overlapping, concepts has led to much unnecessary debate and confusion.

Preference is a capacity intrinsic to a predator and is determined by its behavioral, physiological and morphological properties. A measure of preference is the differential in rates of consumption by a predator of a prey in a single prey species situation and in a multispecies prey situation, independent of compounding factors such as catchability, learning, palatability, toxic substances, prey escape mechanisms, etc. Therefore, preference can only be measured in conditions where prey availabilities can be manipulated and presented to a predator in a uniform manner. This means under laboratory conditions except in rare conditions. Because the techniques for measuring preference (Rapport and Turner 1970; Manly et al 1972) are inappropriate for use here, they will not be discussed further. However, the use of a selectivity coefficient for the analysis of predation experiment results in a loss of information that could be gained through use of more sophisticated tests.

Selectivity is a measure of the probability of a predator taking a particular species of prey once that prey species has been sighted. If a predator is taking all prey species at exactly the proportions that they occur in the environment, then the predator is nonselective. As the distribution of the predator's diet deviates from the distribution of the prey environment, the predator is being more selective. Therefore it

is a critical requirement that any measure of selectivity must be independent of the probability of sighting a prey (i.e. independent of a prey species' abundance). The appropriate measure of selectivity is some relationship between the portion of some prey species in a predator's diet to the portion of the same species in the prey environment. This is a quality that is measurable under field conditions where true preference is not. The confusion arises when one calculates measures of selectivity and then applies them as if they were measures of preference. Many things--learning, local predators, group behavior, catchability, etc.--have combined with preference to determine a predator's selectivity and these other factors cannot be ignored. A relative hierarchy of prey for a particular type of habitat is all that can be obtained from selectivity indices. The ability to predict what a predator will take under radically different conditions requires the investigation of preference.

When analyzing selectivity, there are several major problems with sampling that are encountered regardless of the index used. The first group of interrelated problems centers around sampling the prey species. Marine species tend to be distributed in a patchy manner. While this is probably a larger problem with planktonic prey (O'Brien and Vinyard 1974), it is still a major consideration studying fish that feed on the benthos. For example, five different sets of nine replicate core samples from an open-sand habitat were analyzed for patchiness using a measure based on the mean crowding statistic (Lloyd 1967). In those five sets, the percent of species that were found to deviate from a random distribution to a patchy one was 54%, 57%, 42%, 57% and

37%. The difficulties of sampling patchy distribution have been discussed extensively (Longhurst 1959). Another major problem is whether or not one has actually sampled the prey of a particular predator. An example would be two fish of different species in direct contact with the bottom very close to each other. One fish may be a browser and the other an ambushing predator. These two fishes have very different prey, and one method of sampling will not adequately sample both prey environments. Finally a predator's selectivity is measured as a function of diet versus prey in the environment. If a predator's feeding activity significantly changes the amount of prey in the environment, it would bias a selectivity index. This is rarely a problem in field studies, since prey is usually present in large enough numbers that the effect of any single feed period is negligible. Any of these problems can have major effects on the accuracy of the estimates of prey abundance and therefore, feeding selectivity.

The second group of problems involves obtaining an unbiased sample of a predator's diet. Gannon (1976) has shown the problems that can result from differential digestion rates. Soft-bodied organisms could be digested so much more rapidly than hard-bodied ones that they would be underrepresented in stomach contents. Like prey species in the environment, the distribution of stomach contents of a predator also tend to be distributed in a patchy manner. The stomach contents of rock wrasse (n=13), senorita (n=15) and sheephead (n=13) which were collected at the same time, were individually analyzed for patchiness using the

mean crowding measure. The percents of individuals of each species that had patchy distributions in stomach contents were 80% for the rock wrasse, 82% for the senorita and 100% for the sheephead. This means that variances for these values may be much higher than expected for normal distributions. The same problems discussed in relation to patchy distributions of prey species (i.e. high variability, the need for large numbers of samples and the use of nonparametric statistical tests) apply here and have been discussed elsewhere (Adams 1982). Finally when data with these type of patchy distributions are used to calculate ratio estimators, such as selectivity coefficients, the distribution of these ratios are skewed and not normally distributed (Kendall and Stuart 1969).

Review of Current Indices

The indices that are commonly used to measure selectivity are listed below:

Forage Ratio	-	$F = r/p$	(1) (Savage 1931)
Ivlev's Electivity	-	$E = \frac{r - p}{r + p} = \frac{F - 1}{F + 1}$	(2) (Ivlev 1961)
Strauss' Linear Index	-	$L = r - p$	(3) (Strauss 1979)
Jacobs' Q Index	-	$Q = \frac{r(1 - p)}{p(1 - r)}$	(4) (Jacobs 1974)
Jacobs' D Index	-	$D = \frac{r - p}{r + p - 2rp} = \frac{Q - 1}{Q + 1}$	(5) (Jacobs 1974)

where r = the percent of a prey species in the diet and

p = the percent of a prey species in the environment.

Ivlev's electivity and Jacobs' D are manipulated versions of the forage ratio and Jacobs' Q index respectively so that they are bounded to a range between -1 and $+1$. Both the electivity and Jacobs' D indices are supposedly "linear" with respect to their simpler version which means they have a uniform response between these boundaries. In terms of popularity, the forage ratio was predominantly used in the few feeding studies in which prey abundances were sampled prior to the mid-1960's. At that time, the electivity index became popular and is still the only index in common use. Because of the popularity of these two indices, they will be dealt with in greater detail. Jacobs' and Strauss' indices are rather recent developments and their use, although increasing, is still limited. Many other measures have been suggested but none of these have been widely accepted by other authors.

The criticism of the forage ratio which lead to development of the electivity index was: a) that the forage ratio was open-ended in "positive selection" (it ranged up to infinity) and b) that the forage ratio was unsymmetrical (it ranged from 0 to 1 for "negative selection" ($r - p > 0$) and from 1 to infinity for "positive selection" ($r - p < 0$)). It is shown below that by manipulating the forage ratio into the electivity index these problems are not solved, but merely transformed into a less obvious form. To obtain symmetry in the sense that is discussed above, a more appropriate approach would be to use the logarithm of the forage ratio. Both criticisms stem from an attempt to establish an absolute measure of preference rather than a

relative index in which a prey species' selectivity is measured relative to the selectivity with which other prey species are taken. A more serious criticism of the forage ratio is that its value changes with changes in the relative abundances of prey in the environment. For example, take a hypothetical predator that will eat every individual of prey type A it finds, but only every other individual of prey type B and only every fourth individual of prey type C. In a hypothetical first prey environment, prey type A makes up 33%, prey type B 33% and prey type C 33% of the relative abundances. Then the forage ratio for prey type A would be 1.72, for B 0.86 and for C 0.43. In a hypothetical second prey environment, prey type A makes up 10%, prey type B 30% and prey type C 60%. Now the forage ratio for A is 2.50, for B is 1.25 and for C is 0.63. These differences in forage ratios mean that comparisons cannot be made using this index between predators feeding in different prey environments.

The electivity index (E) was developed to overcome the problem of the forage ratio by being bounded (ranging from -1.0 to +1.0) and by being symmetrical (i.e. the point $r = p$ is the midpoint between the two boundaries). The characteristics of the boundaries of the electivity index are that a) maximum "positive selection" ($E = +1.0$) only occurs when the predator's diet only contains one type of prey and that type of prey is absent from the environment and b) maximum "negative selection" ($E = -1.0$) only occurs when a prey is absent from the diet. Boundry values should represent predators feeding heavily on rare prey as on boundry and predators feeding very lightly or not at all as the

other The boundaries of the electivity index are likely to be result of factors other than the predator's selective feeding behavior, and should be regarded with extreme care.

There are several other points that should be made about the electivity index. The first is that it is a symmetrical index. Therefore the values of E are equal and opposite when the values of r and p are reversed or if E equals A when the value of r is a , and the value of p is b , then E will equal $-A$ when r is b and p is a . The second point is that E values based on species with low abundances in the diet or in the prey environment will change more dramatically as the result of small changes in r or p than E values based on abundant species. For example, if $r = 0.05$ and $p = 0.04$, then $E = 0.11$, but if r is increased by 0.05 , and $r = 0.10$ and $p = 0.04$, then $E = 0.43$. For larger values of r and p where $r = 0.50$ and $p = 0.40$, $E = 0.11$, and if r is increased by 0.05 , and $r = 0.55$ and $p = 0.40$, then E only increases to 0.16 . In other words, E values based on abundant species will be less sensitive to minor errors in estimates of diet or prey environment than will E values from rarer species. This is generally true for ratio estimators. Finally, the electivity index, since it is a transformed version of the forage ratio, suffers the same problem with differences in prey abundance. Using the hypothetical example from above, for the two prey environments, the electivity for prey type A would have changed from $+0.26$ to $+0.43$, for prey type B from -0.09 to $+0.11$ and for prey type C from -0.40 to -0.23 .

Strauss (1979) has pointed out that ratio variables commonly have distributions that deviate from normality. Because of this,

he feels that the compound ratio nature of both the forage ratio and electivity index will result in significant bias. Making the assumption that r and p are normally and independently distributed, Strauss proposed a new index which he feels is normally distributed, L (Eq. 3), as a replacement for Ivlev's electivity index. Since both stomach and prey data are already in the form of ratios, the argument that the ratio nature of the forage ratio and the electivity index will add large amounts of bias is not convincing. This was investigated numerically by calculating these indices for 41 black perch, Embiotoca jacksoni. For each of the eleven prey which occurred consistently (more than ten times), tests of kurtosis were performed (Table 1) to see if the indices were leptokurtic (more concentrated around the mean). Strauss' L deviated from normal in seven of eleven cases which was the largest number of deviations for any index. It was the most kurtic in four cases and the least in three. The performance of this index in relation to normality is no better than the other indices. Strauss fails to recognize the large inherent degree of patchiness in both the diet and prey environment, and their contribution to the distribution of the indices. Strauss' assumption of independence of r and p means that the presence of a prey in a fish's stomach is independent of its occurrence in the environment, an assumption that is difficult to accept. Since the assumption is suspect, then use of his variance estimators for the forage ration and electivity index may be misleading. Strauss' caution in use of parametric test, especially the t test, with selectivity indices seems

Table 1. Tests for kurtosis for prey of black perch (Embiotoca jacksoni) for several selectivity indices.

Species	F	E	Q	D	L
<u>Polychaeta</u>	6.28*	3.71*	6.26*	3.71*	3.47*
<u>Paracerceis</u> sp.	10.73*	2.36	10.71*	2.31	9.06*
<u>Gammaridea</u>	3.94*	14.85*	5.58*	16.64*	3.03*
<u>Ampithoe</u> sp.	1.93	1.68	2.22	1.72	4.91*
<u>Ericthonias braziliensis</u>	4.69*	2.14	4.31*	2.14	7.74*
<u>Hyale frequens</u>	6.33*	3.60*	7.60*	3.92*	3.59*
<u>Jassa falcata</u>	1.74	1.98	1.72	1.96	1.77
<u>Photis</u> sp.	3.56*	5.09*	2.83	5.05*	1.97
<u>Crisia maxima</u>	1.21	1.53	1.31	1.53	2.27
<u>Thalamoporella californica</u>	2.29	1.94	2.29	1.91	2.02
<u>Trididemnum opacum</u>	3.64*	3.85*	3.90*	3.79*	5.26*

* significantly greater than normal at 95% level

appropriate in view of the magnitude of the tests of kurtosis in Table 1. However, Strauss' statement that his index is suitable for use with parametric tests seems unfounded. If statistically significant answers are required, then one should use some well recognized nonparametric test, such as Chi-square, with known statistical properties. Strauss' index (L) shares the same problems as the forage ratio and electivity index in that it is affected by changes in the relative abundances of prey populations. With changes in prey densities in the hypothetical example, Strauss' index changes from +0.24 to +0.15 for prey type A, from -0.04 to +0.08 for prey type B and from -0.19 to -0.23 for prey type C.

Jacobs (1974) was the first to point out the problems with the forage ratio and electivity index with respect to changing prey densities and proposed two new indices, Q (Eq. 4) and D (Eq. 5), to deal with these problems. The index D is a manipulation of Q (see Eq. 5) in the same way that electivity is of the forage ratio. D varies with Q in the same fashion as E varies with F. D, therefore, has the same relationship with Q as does E with F and because of this, D will not be dealt with any further. The problems with Jacobs' indices are with both his theoretical approach and with their numerical performance. Jacobs' derivation of his indices are based on the mortality rates of the prey species. This seems inappropriate since these mortality rates can vary widely due to a large number of factors (i.e. their food, reproductive activity, etc.) which are independent of predation on that species. The primary problem is that Jacobs' derivation only successful deals with the problems of changing

prey densities for a two prey system. For systems with more than two prey, his indices have the same problems as is show below. For a feeding period, let N_i equal the number of prey species i in the environment and Na_i equal the number of prey species i in the predator's gut. Then

$$r_i = \frac{Na_i}{\sum Na_i} \quad (8)$$

and

$$p_i = \frac{N_i}{\sum N_i} \quad (9)$$

Substituting 8 and 9 into the formula for the forage ratio (Eq. 1) and rearranging the variables we have

$$F = \frac{\frac{Na_i}{\sum Na_i}}{\frac{N_i}{\sum N_i}} \quad (10)$$

Which means that the forage ratio is the ratio of number of prey species i eaten divided by the number of prey species i in the environment all divided by the ratio of the number of all prey eaten to the number of all prey in the environment. Now if equations 8 and 9 are substituted into Jacobs' Q (Eq. 4), we have

$$Q = \frac{\frac{Na_i}{\sum Na_i}}{\frac{N_i}{\sum N_i - Na_i}} \quad (11)$$

which is the same ratio in the numerator, but the denominator is now the total number of prey eaten minus those of prey species i

divided by the total number of prey in the environment minus those of prey species i . If there are only two prey in the system, the two values of Q are reciprocal and are unaffected by changes in prey densities. If there are more than two prey species the denominator is no longer constant, then the indices are not simple reciprocals and Q is also affected by changing prey densities, the same as F , E and L . It should also be pointed out that because of this reciprocal nature, in a two-prey situation, the values of Q will be equidistant from each other. In other words for the bounded index (D), the indices will have the same value, only the signs will be reversed. Returning to our hypothetical example, the values of Q in the first environment are 2.67, 0.80 and 0.33; while in the second environment, they are 3.00, 1.40 and 0.40. The corresponding values for D in the first environment are 0.46, -0.11 and -0.50 and in the second environment are 0.50, 0.17 and -0.43. Jacobs' Q index, when applied to only a two-prey situation, has been used at least twice previously by Murdock (1969) and Tinbergen (1960). Since none of the current indices are suitable for comparing selectivity in situations where prey densities are not constant, a new index which meets this requirement is developed below.

A New Measure of Selectivity

The appropriate measure of selectivity is a measure of the relative deviation of the predators diet from the prey environment (see page 5). The selectivity coefficient is then the probability that during the next feeding action, the next prey

taken will be of species i (SC_i , notation used in section will be the same as that common used in optimal foraging theory from Holling 1966). Since the predator will be taking an individual of one of the prey species during the feeding action, the selectivity coefficient will sum to one ($\sum SC_i = 1.0$). One can think of these selectivity coefficients as distorting the prey environment from the actual prey values to the prey environment that this particular predator "sees". If these selectivity coefficients are all constant at a value of one divided by the number of prey species, then the predator is not selective. As the selectivity values differ from this constant, the predator is more selective.

In contrast, the probability of a prey species i being eaten (SE_i) is a function of the probability of predator encountering a prey of species i (EN_i), the probability of a member of prey species being taken in any one feeding action (SC_i), and the number of feeding actions (T , this is also the length of the feeding period). The probability of a prey being eaten by specific predator (SE_i) is equivalent to the proportion of the total feed eaten that was taken from species i (that is r_i), so

$$SE_i = f(EN_i, SC_i).$$

Given the constraint $\sum SE_i = 1.0$ and Equation 8, then

$$SE_i = r_i = \frac{Na_i}{\sum Na_i} \quad (12)$$

where Na_i = the number of prey of species i taken. It is assumed that the encounter probability, EN_i , is proportional to the

number of prey of species i divided by the summation of the numbers of all prey species,

$$EN_i = \frac{N_i}{\sum N_i} \quad (13)$$

where N_i = the number of prey species i in the environment.

The simplest and most common assumption about the relationship between prey density and the number of prey eaten is that during a feeding period, the number of prey eaten (Na_i) is a linear function of prey density (N_i) (Holling 1966)

$$Na_i = N_i SC_i T. \quad (14)$$

Dividing both sides by N_i

$$SC_i T = \frac{Na_i}{N_i}$$

and summing both sides of the expression

$$\sum SC_i T = \frac{\sum Na_i}{\sum N_i}$$

then dividing the first expression by its summation

$$\frac{SC_i T}{\sum SC_i T} = \frac{\frac{Na_i}{N_i}}{\frac{\sum Na_i}{\sum N_i}} \quad (15)$$

Since $\sum SC_i = 1.0$ and the diet is restricted to one feeding period so that T is a constant, then

$$SC_i = \frac{\frac{Na_i}{N_i}}{\frac{\sum Na_i}{\sum N_i}}$$

and from the definition of the forage ratio (F) (Eq. 10)

$$SC_i = \frac{F_i}{\Sigma F_i} \quad (16)$$

A similar approach to measuring selectivity was suggested by O'Neill (1969) and later by Paloheimo (1979). The mathematics of this index are complex, and therefore not easily evaluated, but for the hypothetical predator in first environment, the index values are 0.57, 0.29 and 0.14 and in the second environment 0.57, 0.29 and 0.14. If a version of the index which is bounded between -1 and +1 with a midpoint at 0 is desired, then SC_i can be transformed to new coefficient (SCL_i) in the same manner as the forage ratio is transformed to electivity coefficient,

$$SCL_i = \frac{SC_i - \frac{1}{n}}{SC_i + \frac{1}{n}}$$

where n = the number of prey species. This trades the advantage of a bounded index for the disadvantages of nonlinear response in the same fashion as described for the forage ratio and electivity index.

FISH FEEDING

Introduction

The focus of this modeling study is the fish which feed on the benthos in nearshore habitats at Catalina Island. This section is a more detailed review of these fish's feeding dynamics and is presented here for three reasons. The first is to provide the reader with the necessary background to understand the model. This is a summary of both a number of publications (Hobson and Chess 1978, Hobson et al. 1981, in prep.) and unpublished data. The second is to give the reader an overall view of the community. This community structure is what defines the problem that is to be modeled and is critical to understanding of the model. Lastly, this section illustrates some of the inherent problems involved in modeling. The problems in translating the model structure into a representation of a community (i.e., parameter estimation) are always difficult and demonstrate the need to balance generalization with reality.

The problems are best illustrated by the calculation of selectivity coefficients. Selectivity coefficients are a central feature of the model and therefore their calculation deserves attention. Selectivity coefficients are only calculated for gut samples which have accompanying invertebrate samples taken on the same day. Invariably, there are some prey items found in the gut contents that do not occur in the invertebrate collections and these are excluded from the selectivity calculations. Another problem is that because of the way the invertebrate collections were made, there are very few collections for fish or algae as

prey. Finally, selectivity coefficients for calanoid copepods are artificially high because while they only occur in small numbers in the benthic collections, which are used for calculations, they are very abundant nearby in the water column.

Painted Greenling, Oxylebius pictus

Painted greenling is a small (rarely larger than 152 mm, Miller and Lea 1972) hexagrammid. The species has a sharply pointed snout with a terminal mouth. This fish is strictly demersal and lacks an air bladder (Quast 1965). The fish is not gregarious and is commonly motionless on rocky bottom. This fish is extremely pugnacious and has been observed to dart off the bottom to nip fish many times its size (Feder et al., 1976). There is some degree of territoriality in its behavior. Previous feeding studies (Quast 1968a) found shrimps and caprellids the most important food items.

At Catalina Island, small crustaceans (gammarid and caprellid amphipods and isopods) make up over 70 percent of diet volume (Table 2). These groups also have uniformly high frequency of occurrences. The other major items in the diet are reptantian and natantian decapods. This accounts for ninety percent of the diet volume of this species. Selectivity coefficients for all of these groups is moderately strong (>0.1), with the exception of strong selectivity (0.2) for caprellid amphipods.

Kelp Bass, Paralabrax clathratus

Kelp bass is the principal target species of sport fisheries

Table 2. The diet of painted greenling, Oxylebius pictus, at Catalina Island (n = 22).

	Average number	Average volume	Average prey size	Frequency of occurrence	Selectivity coefficient
Fish	0.05	2.560	11.00	0.09	0.010
Fish eggs	0.09	1.280	2.00	0.09	0.027
Fish larvae	0.05	1.230	12.00	0.05	0.027
Algae	-	0.147	-	0.05	0.001
Hydrozoa	0.14	0.743	-	0.32	0.265
Polychaeta	0.09	1.920	11.54	0.32	0.038
Gastropoda	0.05	0.098	6.00	0.05	0.004
Bivalvia	0.05	0.984	5.25	0.09	0.005
Pycnogonida	0.05	0.098	4.00	0.05	0.004
Ostracoda	0.27	0.098	0.93	0.09	0.004
Cirripedia	-	0.493	-	0.05	0.027
Tanaidacea	0.18	0.147	3.50	0.05	0.019
Isopoda	4.50	7.743	3.53	0.73	0.098
Gammaridea	21.23	45.437	4.27	1.00	0.107
Caprellidea	11.95	20.430	6.18	0.87	0.226
Reptantia	0.55	7.728	4.69	0.41	0.093
Natantia	0.45	8.762	8.79	0.41	0.059
Bryozoa	0.05	0.098	-	0.05	0.001

Average fish size = 105.2 mm

Minimum fish size = 47.0 mm

Maximum fish size = 133.0 mm

in southern California kelp forests. Its large mouth, fusiform body and broad caudal fin are characteristics typical of a medium-to-large (maximum size 721 mm, Miller and Lea 1972) generalized carnivore. This species is frequently found around kelp forests which it uses for cover. It is strongly "curious" about intrusions into its area, but is not aggressive. Its feeding habitats have been extensively studied from kelp beds near La Jolla, California. (Quast 1968b). Fish under 200 mm (the size of fish used in this study) feed on natantian and reptantian decapods, while caprellid amphipods and fish, primarily anchovies, are also important. Larger fish are primarily piscivorous.

At Catalina, kelp bass of this size feed predominantly on benthic organisms (Table 3). Decapods, primarily natantian, account for nearly fifty percent of the diet volume. Amphipods are another quarter of the diet volume. The larger but less abundant caprellid amphipod is more important in kelp bass than the more common gammarid amphipod. This is the reverse of the situation in the other fishes. The diet volumes of mysids (8%) and fish (5%) mean that a significant portion of the diet of kelp bass comes from prey which are up in the water column.

Opaleye, Girella nigricans

Opaleye is a fish with a small mouth and a compressed perch-like body shape. The teeth of this fish are jointed and the jaw has some replacement of bone by connective tissue (Norris and Prescott 1959). This allows considerable anterior-posterior

Table 3. The diet of kelp bass, Paralabrax clathratus, from Catalina Island (n = 36).

	Average number	Average volume	Average prey size	Frequency of occurrence	Selectivity coefficient
Fish	0.47	4.707	22.50	0.06	0.015
Fish eggs	0.11	1.324	2.00	0.03	0.013
Algae	0.03	0.147	-	0.03	0.001
Hydrozoa	-	0.589	-	0.06	0.027
Polychaeta	-	4.826	-	0.14	0.013
Ostracoda	0.08	0.150	1.15	0.06	0.059
Calanoida	0.08	0.589	2.00	0.06	0.002
Harpacticoida	0.06	0.294	1.00	0.03	0.215
Mysidacea	6.11	8.297	6.00	0.28	0.125
Cumacea	0.03	0.442	4.00	0.03	0.001
Tanaidacea	1.06	3.619	4.07	0.19	0.122
Isopoda	0.39	2.266	4.33	0.17	0.023
Gammaridea	4.53	12.934	3.50	0.61	0.021
Caprellidea	7.83	14.387	5.50	0.47	0.090
Reptantia	0.36	7.914	7.93	0.22	0.076
Natantia	2.56	37.425	9.94	0.69	0.196
Ophiuroidea	0.08	0.088	3.00	0.03	0.003

Average fish size = 115.4 mm

Minimum fish size = 56.0 mm

Maximum fish size = 187.0 mm

tooth movement and it is suggested that this allows the individual teeth to move closely over irregularities of rocks when scraping encrusting organisms loose. Williams and Williams (1954) and Quast (1968a) have found that algae and algal-associated animals make up the bulk of the diet; however, because of a lack of alginase activity in the gut they feel the algae provides no nutritional value.

Algae and associated encrusting hydrozoa dominate (90%) the diet of opaleye (Table 4). Gammarid amphipods are the only other significant food item. These were probably taken during feeding on algae. Selectivity for the encrusting hydrozoans are particularly high. If the opaleye obtain no nutritional value from algae, then seventy-five percent of its stomach volume is not used as food.

Pile Perch, Damalichthys vacca

Pile perch is deep-bodied; however unlike the other embiotocids, it has large, heavy pavement-type pharyngeal teeth (De Martini 1969). This strong digestive mill is adapted to crush hard-shelled animals. The diet of pile perch is over 90% bivalves and gastropods (Table 5) and they are very strongly selected. The other significant diet item is another hard-shelled group, ophiuroids. Hermit crabs, a major part of the diet in other studies (Quast 1968a), were not found in these fish, but did appear in other stomach samples from Catalina.

Black Perch, Embiotoca jacksoni

Black perch is the most abundant embiotocid at Catalina.

Table 4. The diet of opaleye, Girella nigricans, from Catalina Island (n = 12)

	Average number	Average volume	Average prey size	Frequency of occurrence	Selectivity coefficient
Algae	0.33	75.526	-	0.92	0.368
Hydrozoa	-	15.521	-	0.67	0.363
Gastropoda	0.92	0.963	1.83	0.25	0.004
Ostracoda	5.75	0.069	0.68	0.42	0.020
Harpacticoida	4.50	0.043	0.94	0.42	0.138
Cyclopoida	0.08	0.008	1.00	0.08	0.001
Isopoda	0.42	0.353	2.00	0.17	0.037
Gammaridea	6.83	4.895	2.55	0.83	0.014
Caprellidea	0.83	0.206	4.00	0.33	0.002
Reptantia	0.08	2.150	9.00	0.08	0.035
Bryozoa	-	0.534	-	0.25	0.020

Average fish size = 196.7 mm

Minimum fish size = 101.0 mm

Maximum fish size = 255.0 mm

Table 5. The diet of pile perch, Damalichthys vacca, from Catalina Island (n = 18).

	Average number	Average volume	Average prey size	Frequency of occurrence	Selectivity coefficient
Polychaeta	1.00	1.045	8.50	0.38	0.014
Gastropoda	18.38	18.960	3.08	0.75	0.186
Bivalvia	64.50	72.416	8.71	0.88	0.576
Isopoda	0.25	0.130	4.70	0.13	0.001
Gammaridea	1.25	0.392	4.50	0.38	0.001
Ophiuroidea	2.25	6.533	3.50	0.05	0.068
Echinoidea	0.25	0.523	-	0.25	0.155

Average fish size = 188.1 mm
 Minimum fish size = 99.0 mm
 Maximum fish size = 235.0 mm

The diet of this species is dominated (55%) by gammarid amphipods (Table 6). The rest of the dietary volume is rather evenly distributed among a large number of groups. This is significantly different than Quast (1968a) who lists polychaetes as their principal prey. This species has no strongly defined pattern of selectivity. Even gammarid amphipods which make up 50% of the diet are only weakly selected. This suggests that within its restricted prey array, black perch grazes more or less indiscriminately with no one prey strongly selected.

Garibaldi, Hypsypops rubicunda

Garibaldi as an adult is a brilliant orange deep-bodied fish. Adults are strongly territorial (Clark 1970). These territories are defended year-round and include a feeding area and for males, a breeding site. Previous feeding studies have shown encrusting groups such as porifera, hydrozoa and bryozoa to be the principal components of the diet. Although algae is frequently found in the gut, it was apparently passed through to the intestine unaltered.

Garibaldi at Catalina Island had algae in every fish taken and it averaged fifty percent of the diet volume (Table 7). Bryozoa, hydrozoa and ascidians, all typical encrusting forms, make up the bulk of the rest of the diet. Porifera which was the principal diet item in Clarke's study off La Jolla is not important here. However, its relatively high selectivity value indicates that this may have been due to differences in availability.

Table 6. The diet of black perch, *Embiotoca jacksoni*, from Catalina Island (n = 22).

	Average number	Average volume	Average prey size	Frequency of occurrence	Selectivity coefficient
Algae	-	1.682	-	0.42	0.004
Foraminifera	1.68	0.188	1.17	0.32	0.077
Porifera	0.03	0.003	-	0.03	0.001
Hydrozoa	-	0.074	-	0.13	0.192
Polychaeta	7.00	7.505	12.08	0.84	0.022
Polyplacophora	0.08	0.003	4.00	0.03	0.001
Gastropoda	15.68	2.189	2.56	0.68	0.024
Bivalvia	2.97	1.225	4.71	0.58	0.012
Ostracoda	9.97	1.326	1.68	0.74	0.012
Harpacticoida	0.39	0.033	1.29	0.03	0.002
Cyclopoida	0.19	0.003	1.00	0.03	0.004
Mysidacea	0.06	0.070	6.50	0.06	0.011
Cumacea	0.06	0.006	2.00	0.06	0.009
Tanaidacea	10.32	2.377	2.86	0.74	0.153
Isopoda	12.37	3.246	3.77	0.81	0.019
Gammaridea	162.87	54.866	4.08	0.97	0.050
Caprellidea	5.67	2.625	7.27	0.52	0.044
Reptantia	1.09	2.626	6.96	0.48	0.024
Natantia	1.23	3.962	9.50	0.42	0.036
Bryozoa	-	3.059	-	0.58	0.005
Ophiuroidea	4.03	6.884	3.17	0.52	0.087
Echinoidea	0.02	0.349	2.20	0.65	0.103
Ascidiacea	-	5.641	-	0.03	0.034
Entoprocta	-	0.003	-	0.03	0.015

Average fish size = 143.0 mm

Minimum fish size = 88.0 mm

Maximum fish size = 184.0 mm

Table 7. The diet of garibaldi, Hypsypops rubicundus, from Catalina Island (n = 12).

	Average number	Average volume	Average prey size	Frequency of occurrence	Selectivity coefficient
Fish	0.50	0.576	8.00	0.08	0.004
Algae	0.17	49.328	-	1.00	0.243
Foraminifera	1.25	1.651	-	0.08	0.035
Porifera	0.25	0.389	-	0.08	0.035
Hydrozoa	-	5.598	-	0.83	0.194
Anthozoa	0.67	3.361	7.00	0.25	0.047
Polychaeta	0.92	1.921	10.00	0.42	0.011
Gastropoda	0.08	0.960	8.00	0.17	0.009
Bivalvia	0.08	0.192	3.00	0.08	0.009
Cephalopoda	0.50	0.192	2.00	0.08	0.011
Ostracoda	0.58	0.048	1.17	0.25	0.006
Harpacticoida	0.25	0.020	1.50	0.17	0.007
Cirripedia	-	0.960	-	0.08	0.026
Tanaidacea	0.17	0.009	2.50	0.08	0.001
Isopoda	0.17	0.020	2.50	0.17	0.001
Gammaridea	8.06	2.083	2.68	0.83	0.025
Caprellidea	0.42	0.317	5.25	0.33	0.001
Reptantia	-	0.192	8.00	0.08	0.060
Bryozoa	0.17	20.088	-	0.67	0.079
Asteroidea	0.17	3.841	8.00	0.08	0.023
Ophiuroidea	0.17	0.288	4.00	0.08	0.010
Ascidacea	0.92	7.970	8.50	0.50	0.054

Average fish size = 170.0 mm
 Minimum fish size = 134.0 mm
 Maximum fish size = 235.0 mm

Rock Wrasse, Halichoeres semicinctus

Rock wrasse is one of three wrasses (Labridae) occurring in California temperate waters. The Labridae is predominantly a tropical family. Its body shape is laterally flattened. Its dorsal and anal fins extend almost back to the caudal fin. It has a small mouth (about 5% of total length) with teeth that project forward. Rock wrasse is a sequential hermaphrodite (Feder et al. 1974), changing from female to male. This species spends the night in rock crevices or under algae (Hobson et al. 1981). Fish under 100 mm feed entirely on plankton (Hobson et al. in prep.) and will not be dealt with here.

Rock wrasse in the size range 100 to 150 mm are taking benthic species with almost no trace of exclusively planktonic organisms (Table 8). Gammarid and caprellid amphipods are the dominant groups (48%), but other benthic algae-associated groups such as gastropods (16%) and bryozoa (15%) are also important. Fish over 150 mm are benthic foragers who are taking a larger range of prey (Table 9). Their diet has shifted more to prey that are taken from rock surfaces and sand rather than those strongly associated with algae. Gammarid and caprellid amphipods are still the largest diet item (24%) but are considerably reduced in importance. Polychaetes (11%) and ophiuroids (10%) are major prey to fish this size. Shifts in prey taken follow a similar pattern with selectivity for gammarid amphipods which is decreasing in larger fish.

Senorita, Oxyjulis californica

Senorita is another commonly occurring wrasse at Catalina

Table 8. The diet of smaller (> 150 mm) rock wrasse, Halichoeres semicinctus, from Catalina Island (n = 11).

	Average number	Average volume	Average prey size	Frequency of occurrence	Selectivity coefficient
Fish eggs	1.27	0.462	-	0.18	0.001
Algae	-	0.839	-	0.27	0.002
Hydrozoa	-	0.009	-	0.09	0.035
Polychaeta	0.64	6.917	-	0.27	0.033
Gastropoda	7.27	16.430	2.58	0.55	0.028
Bivalvia	3.45	3.791	3.00	0.82	0.071
Pycnogonida	0.91	0.277	6.00	0.09	0.001
Ostracoda	0.55	0.286	1.67	0.27	0.180
Cirripedia	0.09	0.462	-	0.09	0.001
Cumacea	1.64	0.922	3.13	0.18	0.033
Tanaidacea	2.82	2.029	3.13	0.36	0.013
Isopoda	0.82	0.553	3.33	0.27	0.029
Gammaridea	65.27	42.020	3.00	0.91	0.036
Caprellidea	14.91	6.550	6.25	0.55	0.057
Reptantia	0.18	1.844	6.00	0.18	0.102
Natantia	-	1.003	-	0.18	0.110
Bryozoa	20.91	15.406	-	0.27	0.102
Ophiuroidea	0.91	4.336	2.50	0.36	0.144
Ascidacea	0.36	2.306	-	0.09	0.033

Average fish size = 133.4 mm
 Minimum fish size = 106.0 mm
 Maximum fish size = 150.0 mm

Table 9. The diet of large (< 150 mm) rock wrasse, Halichoeres
semicinctus, from Catalina Island (n = 43).

	Average number	Average volume	Average prey size	Frequency of occurrence	Selectivity coefficient
Fish eggs	1.72	1.100	2.13	0.14	0.029
Algae	0.07	4.783	-	0.53	0.034
Foraminifera	0.23	0.057	1.80	0.14	0.016
Porifera	0.05	0.153	6.00	0.07	0.056
Hydrozoa	-	0.150	-	0.07	0.005
Nemertea	0.02	0.050	1.58	0.02	0.011
Polychaeta	3.81	11.414	9.58	0.67	0.025
Polyplacophora	0.07	0.030	3.50	0.07	0.003
Gastropoda	7.60	7.082	3.83	0.84	0.031
Bivalvia	3.12	5.563	4.66	0.67	0.054
Pycnogonida	0.09	0.251	7.00	0.07	0.004
Ostracoda	1.98	0.525	1.30	0.30	0.001
Harpactacoida	0.23	0.053	1.50	0.02	0.110
Cirripedia	0.02	0.325	-	0.07	0.002
Mysidacea	0.07	0.124	4.00	0.02	0.004
Cumacea	0.26	0.055	2.50	0.09	0.002
Tanaidacea	0.63	0.278	3.00	0.16	0.054
Isopoda	2.72	3.340	5.61	0.44	0.021
Gammaridea	29.14	17.007	3.54	0.88	0.029
Caprellidea	10.12	5.884	7.96	0.33	0.112
Reptantia	0.74	9.130	9.53	0.47	0.041
Natantia	0.19	1.428	8.25	0.14	0.038
Bryozoa	0.16	14.428	-	0.63	0.067
Asteroidea	0.07	0.175	8.00	0.02	0.002
Ophiuroidea	1.58	10.456	3.19	0.49	0.097
Echinoidea	0.40	1.028	4.67	0.21	0.133
Ascidiacea	0.98	5.280	5.93	0.40	0.020

Average fish size = 178.3 mm

Minimum fish size = 151.0 mm

Maximum fish size = 218.0 mm

Island. It has a more typically fusiform, cigar-shaped body than rock wrasse and is considerably smaller. *Senorita* is a diurnal feeder and its habit of burrowing in sand soon after sunset is well documented (Bray and Ebeling 1979; Hobson et al. 1981). This is probably the most common fish species involved in "cleaning" activity in nearshore California waters (Hobson 1971). Fish under 100 mm feed on plankton (Hobson et al., in prep.) and again will not be dealt with here.

Senorita between 100 and 150 mm have a mixed diet (Table 10). Copepods, primarily calanoids, still make up almost twenty percent of the diet. This means that planktivorous feeding is still a significant part of the diet. However, the rest of the diet is made up of algae and rock associated groups. The diet of fish over 150 mm (Table 11) is dominated by bryozoa (30%), polychaetes (20%), and algae (18%) and the exclusively planktonic groups are virtually absent. Also mollusks appear in the diet in significant amounts. Decapods are virtually absent from the diet of fish in both size classes.

The diet of *Senorita* has a clear progression with size. Smaller fish are exclusively planktivorous. As fish size increases, the diet moves through a transition from plankton to small crustaceans on the benthos. Larger fish are feeding exclusively on rock or algae-oriented substrate.

Sheephead, *Semicossyphus pulcher*

Sheephead is the third member of the wrasse family at Catalina Island. This fish is also a sequential hermaphrodite (Feder et al. 1974). It, like other wrasses, rests on the bottom

Table 10. The diet of smaller (> 150 mm) senorita, Oxyjulis californica, from Catalina Island (n = 25).

	Average number	Average volume	Average prey size	Frequency of occurrence	Selectivity coefficient
Fish eggs	0.24	0.696	1.50	0.04	0.002
Algae	1.66	9.702	5.00	0.48	0.071
Porifera	-	0.041	-	0.04	0.001
Hydrozoa	-	0.205	-	0.04	0.207
Polychaeta	8.40	10.357	3.50	0.36	0.085
Gastropoda	1.36	0.778	2.25	0.24	0.005
Veleger	7.34	0.618	0.68	0.08	0.003
Bivalvia	1.08	0.294	1.55	0.16	0.014
pyncogonida	0.40	3.643	6.33	0.12	0.001
Cladocera	23.08	4.503	0.89	0.16	0.001
Ostracoda	0.12	0.041	1.00	0.04	0.001
Calanoida	48.88	10.725	1.19	0.36	0.074
Harpactacoida	0.08	0.005	0.85	0.08	0.007
Cyclopoida	15.84	2.538	0.89	0.24	0.007
Caligoida	0.84	3.807	2.75	0.08	0.074
Cirripedia	21.40	6.595	0.96	0.24	0.007
Tanaidacea	0.08	0.041	-	0.04	0.002
Isopoda	10.36	6.185	3.06	0.40	0.095
Gammaridea	18.68	17.193	2.93	0.60	0.032
Caprellidea	1.68	4.830	6.79	0.36	0.123
Euphausiacea	2.24	0.205	1.25	0.08	0.001
Natantia	0.04	0.004	4.00	0.04	0.006
Insecta	0.04	0.041	2.00	0.04	0.001
Bryozoa	1.76	16.870	0.90	0.52	0.181
Ophiuroidea	-	0.082	-	0.04	0.001
Echinoidea	-	0.041	-	0.04	0.001

Average fish size = 138.0 mm

Minimum fish size = 108.0 mm

Maximum fish size = 150.0 mm

Table 11. The diet of large (< 150 mm) senorita, Oxyjulis californica, from Catalina Island (n = 18).

	Average number	Average volume	Average prey size	Frequency of occurrence	Selectivity coefficient
Fish eggs	0.39	0.521	1.75	0.17	0.002
Algae	5.22	17.724	8.25	0.61	0.139
Polychaeta	44.22	20.456	3.88	0.67	0.103
Polyplacophora	0.06	0.058	4.00	0.06	0.004
Gastropoda	10.00	6.230	2.63	0.22	0.039
Bivalvia	2.22	3.370	3.33	0.17	0.005
Cladocera	13.06	2.790	0.77	0.17	0.015
Ostracoda	0.06	0.058	2.00	0.06	0.001
Calanoida	1.17	0.348	2.00	0.11	0.178
Harpactacoida	1.72	0.878	1.00	0.11	0.019
Cyclopoida	-	0.058	-	0.06	0.025
Caligoida	0.06	0.058	0	0.06	0.025
Mysidacea	0.11	0.058	0.50	0.06	0.001
Isopoda	3.78	3.027	5.06	0.28	0.015
Gammaridea	5.50	4.998	4.64	0.56	0.013
Caprellidea	23.22	6.335	8.67	0.28	0.049
Natantia	-	0.571	-	0.06	0.002
Bryozoa	2.00	29.644	-	0.78	0.182
Ophiuroidea	-	0.407	-	0.06	0.152
Echinoidea	-	0.116	-	0.06	0.025
Ascidacea	-	1.976	-	0.22	0.080

Average fish size = 167.8 mm

Minimum fish size = 151.0 mm

Maximum fish size = 197.0 mm

among the rocks at night (Hobson 1968; Ebeling and Bray 1979). occasionally, juvenile and adult Sheephead are observed resting with a transparent mucus envelope (Turner et al. 1969; Wiley 1974). The function of the mucus envelope is unknown, but other authors have suggested that its purpose is predator avoidance. Like the other wrasses, sheephead also has protruding or "buck" teeth, but it also has large, strong pharyngeal teeth (Feder et al. 1974).

Almost half of the diet of sheephead under 150 mm is gammarid amphipods (Table 12). Polychaetes, bivalves, gastropods and both reptantian and natantian decapods make up the rest of the diet. In fish over 150 mm, only 7% of their diet is gammarid amphipods (Table 13). Heavy armored groups such as bivalves, gastropods, and reptantian decapods (hermit crabs living inside abandoned gastropod shells) make up the differences in diet volume. As the fish grows to full size, it utilizes prey that require its large pharyngeal teeth. Fish especially under 50 mm collected from other habitats have a strong plankton component in their diet (Hobson et al., in prep.)

Island kelpfish, Alloclinus holderi

Island kelpfish is a small (maximum length 220 mm, Miller and Lea 1972), cryptically colored fish which sits on rocks during the day and retires to shelter at night (Hobson et al. 1981). It has a typical clinid body with a tubular shape, extended dorsal and anal fins, and rounded caudal fin. Quast (1968a) reported that it feeds primarily on gammarid amphipods.

Table 12. The diet of small (> 150 mm) sheephead, Semicossyphus pulcher, from Catalina Island (n = 16).

	Average number	Average volume	Average prey size	Frequency of occurrence	Selectivity coefficient
Fish eggs	2.00	1.714	2.00	0.29	0.024
Nemertea	0.14	2.143	2.00	0.14	0.030
Polychaeta	1.43	14.286	10.25	0.57	0.086
Polyplacophora	0.14	0.143	6.00	0.14	0.001
Gastropoda	2.43	1.600	2.50	0.57	0.030
Bivalvia	4.57	13.143	3.70	0.71	0.080
Ostracoda	1.43	0.743	1.17	0.43	0.076
Cyclopoida	0.14	0.014	1.00	0.14	0.001
Caligoida	-	0.143	-	0.14	0.001
Tanaidacea	0.86	0.714	3.00	0.24	0.065
Isopoda	0.71	2.443	4.00	0.57	0.028
Gammaridea	24.57	47.143	2.60	0.86	0.057
Caprellidea	0.71	1.429	5.50	0.14	0.005
Reptantia	0.86	5.300	4.50	0.43	0.057
Natantia	1.43	6.286	6.50	0.57	0.043
Ophiuroidea	1.43	0.714	-	0.14	0.046
Echinoidea	0.14	1.714	-	0.29	0.215

Average fish size = 107.7 mm
 Minimum fish size = 65.0 mm
 Maximum fish size = 150.0 mm

Table 13. The diet of large (< 150 mm) sheephead, Semicossyphus pulcher, from Catalina Island (n = 38).

	Average number	Average volume	Average prey size	Frequency of occurrence	Selectivity coefficient
Fish	0.32	0.954	7.00	0.05	0.019
Algae	-	1.892	-	0.32	0.016
Foraminifera	0.08	0.003	1.00	0.03	0.029
Porifera	0.21	2.714	10.00	0.26	0.046
Hydrozoa	0.08	0.030	-	0.05	0.016
Anthozoa	0.03	0.109	7.00	0.05	0.120
Nemertea	0.03	0.003	4.00	0.03	0.001
Polychaeta	1.82	11.322	12.46	0.74	0.098
Polyplacophora	0.05	0.414	9.00	0.05	0.007
Gastropoda	4.74	8.373	5.33	0.68	0.096
Bivalvia	9.76	23.525	7.17	0.84	0.152
Pycnogonida	0.24	0.329	7.25	0.05	0.008
Ostracoda	0.24	0.070	1.75	0.60	0.001
Cirripedia	0.26	1.618	8.00	0.13	0.057
Cumacea	0.08	0.055	8.00	0.03	0.001
Tanaidacea	0.66	0.301	2.83	0.08	0.002
Isopoda	1.47	1.927	5.82	0.39	0.013
Gammaridea	11.71	6.692	5.16	0.68	0.013
Caprellidea	0.26	0.247	8.00	0.05	0.025
Reptantia	1.66	20.862	13.88	0.34	0.066
Natantia	0.74	4.826	14.11	0.34	0.044
Bryozoa	1.37	4.871	-	0.42	0.015
Ophiuroidea	0.50	1.453	3.75	0.13	0.038
Echinoidea	0.47	5.456	13.00	0.26	0.097
Holothuroidea	0.34	0.030	-	0.05	0.016
Ascidiacea	-	1.946	-	0.50	0.009

Average fish size = 201.3 mm

Minimum fish size = 151.0 mm

Maximum fish size = 394.0 mm

The bulk of the diet of island kelpfish (60%) from Catalina Island is small crustaceans (gammarid and caprellid amphipods and isopods) (Table 14). The caprellids, because of their large size, are much smaller in terms of numbers and therefore much more highly selected. Island kelpfish is one of the few fish that has relatively high selectivity values for gammarids. Virtually the rest of the diet is made up of decapods, primarily natantians. These are also very highly selected. Most of the diet of island kelpfish is made up of a few prey groups which are common but not highly selected in the diet of other fish.

Spotted kelpfish, Gibbonsia elegans

Spotted kelpfish is another small (maximum size 157 mm, Miller and Lea 1972) clinid with cryptic coloration. It rests on benthic algae, relatively motionless and, although fully exposed, will often be unnoticed (Hobson et al. 1981). This fish appears to seek shelter at night. Quast (1968a) lists its principal foods as small crustaceans and polychaetes.

Gammarid amphipods dominate the diet of Gibbonsia, making up half of the diet volume (Table 15). Selectivity coefficients for gammarids are higher for this fish than for any other fish. Isopods are the next most important group and again are also more highly selected here than in other fish. Decapods, mostly shrimp-like natantians, make up the rest of the bulk of the diet.

Blackeye Goby, Coryphopterus nicholsii

Blackeye goby is a bottom-dwelling fish. Large numbers rest on sand bottoms in exposed positions in and around rocks. The

Table 14. The diet of island kelpfish, Alloclinus holderi, from Catalina Island (n= 22).

	Average number	Average volume	Average prey size	Frequency of occurrence	Selectivity coefficient
Fish eggs	0.50	1.389	1.00	0.06	0.028
Polychaeta	0.28	3.444	13.00	0.28	0.010
Gastropoda	0.22	1.778	2.45	0.22	0.003
Veleger	0.06	0.056	1.00	0.06	0.001
Bivalvia	0.06	0.111	2.00	0.06	0.004
Ostracoda	0.28	0.289	0.92	0.28	0.006
Harpacticoida	0.10	0.056	0.80	0.06	0.014
Mysidacea	0.06	0.278	4.00	0.06	0.011
Cumacea	-	0.084	-	0.06	0.017
Isopoda	2.17	10.556	3.85	0.61	0.057
Gammaridea	6.61	29.589	3.75	1.00	0.071
Caprellidea	1.50	20.167	8.15	0.38	0.145
Reptantia	0.22	7.333	4.50	0.54	0.356
Natantia	0.89	25.222	12.54	0.54	0.278

Average fish size = 73.3 mm

Minimum fish size = 58.0 mm

Maximum fish size = 100.0 mm

Table 15. The diet of spotted kelpfish, Gibbonsia elegans, from Catalina Island (n = 13).

	Average number	Average volume	Average prey size	Frequency of occurrence	Selectivity coefficient
Fish	0.08	0.310	8.00	0.08	0.001
Fish eggs	0.31	0.396	2.00	0.08	0.001
Algae	-	0.317	-	0.15	0.015
Foraminifera	0.08	0.396	1.56	0.08	0.308
Polychaeta	-	0.633	-	0.15	0.025
Gastropoda	0.54	1.268	2.56	0.15	0.011
Cladocera	-	0.317	-	0.15	0.002
Ostracoda	0.09	0.238	1.00	0.08	0.002
Calanoida	0.08	0.238	3.00	0.08	0.001
Cirripedia	0.08	0.008	1.00	0.08	0.001
Isopoda	3.38	18.225	4.65	0.85	0.196
Gammaridea	19.77	50.000	4.50	1.00	0.148
Caprellidea	0.62	4.913	7.88	0.38	0.083
Reptantia	0.62	8.638	6.25	0.54	0.104
Natantia	0.69	14.422	7.75	0.54	0.103
Average fish size = 86.8 mm					
Minimum fish size = 46.0 mm					
Maximum fish size = 112.0 mm					

fish's light color blends into sand bottoms making it almost invisible except for its black eyes. Its ventral fins are united, forming a disk on which the fish normally rests on the bottom. Swimming is confined to short spurts, primarily for feeding or defense (Wiley 1973).

Blackeye goby has an extremely varied diet and no one category dominates the diet (Table 16). It is the only species in which ophiuroids are the major diet item. The other primary diet items are gammarids, polychaetes, mollusks, and decapods. Of these major groups, only the ophiuroids and natantian decapods are selected highly.

Table 16 The diet of blackeye goby, Coryphopterus nicholsii, from Catalina Island (n = 41).

	Average number	Average volume	Average prey size	Frequency of occurrence	Selectivity coefficient
Fish	0.10	1.110	5.00	0.08	0.001
Fish eggs	0.23	0.608	2.17	0.08	0.001
Algae	-	0.661	-	0.08	0.021
Foraminifera	0.23	0.449	0.86	0.10	0.123
Porifera	-	0.264	-	0.03	0.017
Nemertea	0.03	0.264	3.00	0.03	0.002
Polychaeta	0.06	14.431	8.29	0.89	0.086
Polyplacophora	0.03	0.661	4.00	0.03	0.002
Gastropoda	1.08	9.541	2.78	0.53	0.037
Bivalvia	0.80	7.797	3.17	0.38	0.021
Pycnogonida	0.08	1.216	4.33	0.08	0.012
Ostracoda	2.00	5.686	1.64	0.58	0.021
Calanoida	1.30	0.661	0.10	0.10	0.084
Harpactacoida	1.48	1.506	1.66	0.20	0.019
Cyclopoida	1.88	2.352	2.49	0.10	0.019
Cumacea	0.55	3.383	3.10	0.25	0.039
Tanaidacea	0.20	0.819	2.92	0.15	0.116
Isopoda	0.33	2.828	5.28	0.23	0.028
Gammaridea	2.83	15.673	2.33	0.58	0.026
Caprellidea	0.68	2.802	4.85	0.28	0.016
Reptantia	0.0	2.511	5.00	0.03	0.037
Natantia	0.13	7.110	11.67	0.10	0.108
Bryozoa	0.13	0.264	0.70	0.08	0.003
Ophiuroidea	0.78	14.080	0.50	0.80	0.087
Echinoidea	0.18	1.312	2.50	0.10	0.075

Average fish size = 67.8 mm

Minimum fish size = 31.0 mm

Maximum fish size = 90.0 mm

MODEL STRUCTURE

Introduction

All models are abstractions of reality and therefore must involve some amount of simplification and assumptions. Along with these simplifications and assumptions, there is some inevitable loss of information which Levins (1966) categories into precision, realism and generality. The goals one has for a model are an integral part of this process. They play a major role in how decisions about the model are made and in which particular category to sacrifice information. The goal of this model is to simulate the feeding dynamics of the diurnal benthic feeders at Catalina Island and then to add a harvesting component to the model. This model is then used to investigate the effects of trophic interactions on the relative efficiency of single species versus multispecies management. In Levins' terminology, we are sacrificing generality to realism and precision, but as long as similar trophic mechanisms are operating in other habitats, the conclusions should be transferable. The second goal of the model is to evaluate the differences between a stochastic feeding model and a deterministic one. For this, the same model except with a deterministic feeding model is constructed and analyzed for single and multispecies harvesting. The results can then be compared to the stochastic model used here.

The model structure is organized around a single community made up of 12 fish species. Three of the fish species are further subdivided into two size groups because of major

differences in their diet. Each size group is treated in the model as if it were a separate species. The major components for each fish species are their feeding (stochastic or deterministic), long term population dynamics, harvesting and changes in prey populations. An initial static model with fixed population sizes is analyzed to investigate the stochastic feeding model. In the static model, fish population sizes are fixed throughout the model run so there is no long term population components. Each of these major components are discussed in detail in later sections. Finally, the different harvesting strategies are developed in detail.

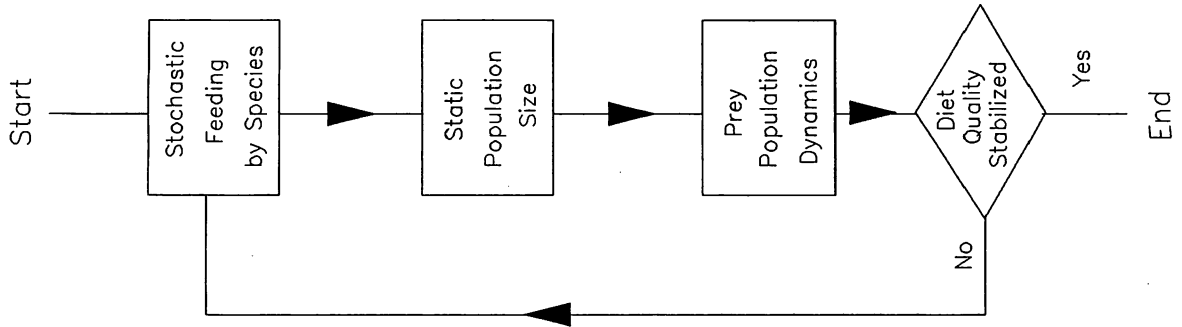
Time Scale

The model cycles through all operations of the major components; feeding, long term population dynamics, harvesting, and renewal of the prey populations. These operations all take place each cycle, but each operation is discrete within that cycle. In the static model, these operations continue until all of the fish species' diet stabilize (not more than 15% change) over three consecutive cycles. In the full model, this continues until all of the fish population sizes stabilize over three consecutive cycles (see flowcharts in Fig. 1).

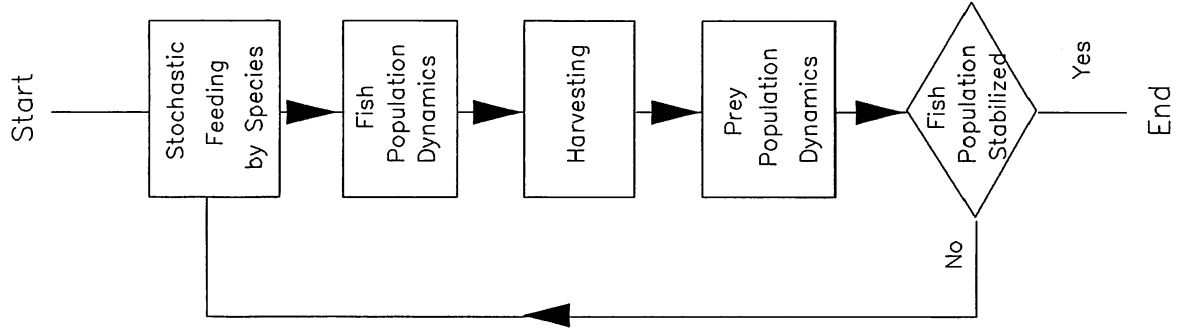
Fish Species

The fish species used in the model are the twelve species discussed in the Fish Feeding section. These include all the species at Catalina which spent a major portion of their time foraging diurnally on benthic substrates. Three species; rock

Static Model



Stochastic Full Model



Deterministic Full Model

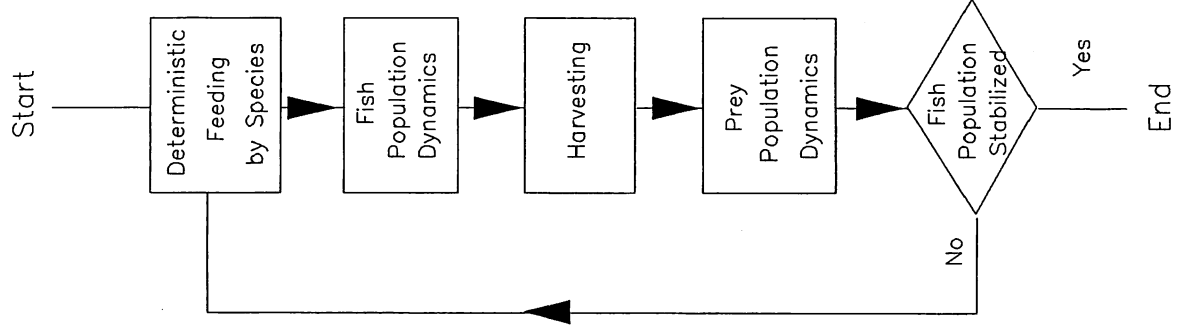


Figure 1. Flowcharts for the three model structures.

wrasse, senorita and sheephead; are split in two distinct size groups corresponding with major shifts in their diet. Each size class will be treated as if it is a separate species. Initial values for population sizes were taken from average values for all line transects.

stochastic Feeding

As mentioned earlier, each operation is discrete within each cycle. In this case, that means that all of the feeding takes place together without interruption due to population changes, harvesting, etc. Within the feeding model, each species feeds in sequence, one feeding action (or prey capture) at a time. This continues until the volume a fish species' gut contents reach that of an average diet observed in nature. At this time, the species drops out of the feeding sequence. This continues until all of the fish have dropped out of the feeding sequence.

Feeding is simulated in the form of a Markov chain. At any time within the feeding cycle, t , a fish species will have just taken a prey of some species i . A decision as to which prey to take at time $t+1$ is limited to one of 42 possible prey groups. The probability that the fish will take one of these 42 prey is dependent on the combination of the number of that prey in the environment at time t (N_i which controls the encounter probability EN_i) and the probability of capture of that prey by that particular predator independent of encounter rate (SC_{ij}). Then a matrix for transition between feeding on one prey type at time t and feeding on another at time $t+1$ is the probability of that prey being eaten by a particular fish predator (SE_{ij}). A

random number between zero and one is generated. This number is compared to the cumulative probabilities of being eaten (SE_{ij}) as a method of selecting the next prey group that is taken. A member of that prey is removed from the prey population and the feeding cycle continues. This process makes the Markov assumption that the probabilities of transition from feeding on prey species at cycle t to feeding on another prey at cycle $t+1$ is only dependent on the state of the environment at cycle t and the predator's selectivity, and is not affected by the condition of factors previous to cycle t (for a formal probabilistic definition of Markov chains, see Bartlett 1966 or Purdue 1979). Probability of capture (SC_{ij}) are calculated as averages from values for individual fish. Outliers were removed before computing the averages.

The daily ration for a fish species is the sum of the number of prey groups taken of ($\sum Na_i$). A fish continues to feed until this daily ration reaches a volume equal to the volume from the average diet from the Fish Feeding section. In the static model, to characterize the diet of a fish species in a single number that represents nutritional value, it is assumed that there is some relationship between the nutritional value of any particular prey and its degree of selectivity (see The Analysis of Feeding Selectivity section, p 3-4, and Holmberg 1978, Rapport 1980). Therefore as the amount of highly selected prey increases within the diet, the nutritional value of the fish species diet increase. A measure of diet quality of fish species j (DQ_j) is then the summation of the prey's selectivity times the volume of

that prey in the fish's diet. This is a measure of the average selectivity of fish species diet and can be compared as increasing or decreasing to some standard value.

Deterministic Feeding

Previous multispecies fisheries models (Anderson and Ursin 1977, Knechtel and Bledsoe 1981, Laevastu and Favorite 1978, Laevastu and Larkins 1981) used deterministic representations of feeding behavior. All of these models used the same general formulation where the fish species' diet is some function of the predator's selectivity times some function of the prey's availability. In the model notation used here, the deterministic feeding equation would be

$$Na_i = SC_{ij}EN_j.$$

and as in stochastic feeding, the fish species will feed until it reaches its average gut volume in nature.

Long Term Population Dynamics

The starting point of any description of long term population dynamics is reproduction or fecundity of the fish. There are many observations of a reduction of fecundity and delays in maturity associated with undernourishment in fish populations (McFadden et al 1965, Leggett and Power 1969, Bagenal 1967, Raitt 1968, and Hodder 1965). Under these circumstances, fecundity would be dependent on nutrition either directly or indirectly through growth. This assumes a relationship between the quality of the diet (or energetic content) of the predator's ration and fecundity. The theoretical mechanism of this

assumption is that as diet quality decreases, energy is conserved at the expense of developing gonadal tissue. There is strong evidence in the literature to support this assumption. Tyler and Dunn (1976) investigated the relationship between six ration levels and ovary condition in winter flounder (Pseudopleuronectes americanus). They found an increasing relationship between ration size and the number of oocytes. So if the ration of these fish in natural environment increased or decreased, the number of oocytes, and presumably reproduction, would increase or decrease. Scott (1962) made similar investigations on rainbow trout (Salmo gairdneri). He also found that reduction in ration resulted in a reduction in the number of eggs brought to maturity. In both of these instances, body weight remained constant at lower rations. Similar results have been obtained from studies on Lebistes reticulatus (Hester 1964), Salmo trutta (Bagenal 1969), Rutilus rutilus (MacKay and Mann 1969) and Gasterosteus aculeatus (Wootton 1973). This is strong evidence that in the face of reduction of diet quality, a fish's adaptive response is to sacrifice egg production and maintain body weight.

In the long term population dynamics of the fish predators, all factors other than the effects of diet and the impact of harvesting are assumed to be constant. Since these rates are constant and populations can not increase or decrease indefinitely, there must be some element of density dependence. The simplest assumption that can be made about density dependence is that birth rates decrease and death rate increase linearly with population size and the combined rate become zero at some

maximum populations size. These two assumptions lead to the classical Verhulst-Pearl logistic equation. The form of the equation is

$$\frac{dP_j}{dt} = r_j P_j \frac{K_j - P_j}{K_j}$$

where P_j = population size of fish species j

K_j = maximum population size of fish species j

r_j = rate of population increase of fish species j .

Implicit in the Verhulst-Pearl logistic equation are three assumptions. 1) All individuals are equivalent; this means that every new individual reduces the actual rate of increase by the same amount. This eliminates any age class effects. 2) r_j and K_j are constants. A procedure for modifying K_j is described below. 3) There is no time lag in the response of the rate of increase to the population size. These assumptions, their problems and attempts to compensate for have been extensively discussed elsewhere (Pianka 1974). Besides its widespread use in ecological literature (Poole 1974), the logistic equation has been widely used in fisheries biology both explicitly (Graham 1953; Larkin 1963, 1965; May et al 1979) and as the general production model (Schaefer 1957; Pella and Tomlinson 1969).

Maximum population size (K_j) is estimated from numbers of fish in the transect counts. The rate of population increase (r_j) is estimated from corresponding values of other fish populations (Bagenal 1978) and the theory of life history strategies (see Part V). In order to incorporate the impact of nutrition on reproduction into the model, the maximum population of the fish is allowed to vary linearly with changes in diet

quality. Annual variation in fecundity of marine fishes varies from 20 to 60 percent (Bagenal 1978). Therefore maximum population size is allowed to increase or decrease in this range with diet quality. For the cases in which a fish is divided into two age classes, the population size of the youngest age class is a nonnegative number calculated from a logistic function using the size of the older age class. The older age class increases by the addition of the younger age class.

Harvesting

The harvesting component of this model is the standard expression of instantaneous fishing mortality

$$\frac{dP_j}{dt} = F_j P_j \quad (\text{Ricker 1975})$$

or

$$P_{j,t+1} = P_{j,t} e^{-F_j}.$$

where $P_{j,t}$ = population size of fish species j at time t

F_j = the instantaneous rate of fishing mortality for fish species j .

This model assumes that the number of fish captured by a fixed amount of gear during a time period is linearly proportional to the number of fish in that population at the beginning of that time period. The effect of different amounts of effort is dealt with by further subdividing the instantaneous rate of fishing mortality

$$F_j = q_j E_j$$

where q_j = catchability coefficient for fish species j ,

E_j = the amount of effort directed toward fish species j .

This is a commonly used approach to modeling harvesting in fisheries mathematics and the characteristics of this equation is discussed elsewhere (Ricker 1975). The amount of effort directed toward a particular species (E_j) is controlled by the management approach (single species vs. multispecies).

Prey Populations

Ideally prey populations should be modeled at the same level of detail as the fish populations. However since this model uses feeding functions based on prey abundances, an operational limitation is imposed that the ultimate resource base, that is the lowest item in the food chain, cannot be modeled using input from the trophic level below. Thus the prey species that are the base of the trophic web cannot be modeled in the same degree of complexity in relation to their feeding activities. Because of this limitation, prey populations are represented by logistic models with fixed constants. The constant r_i is again estimated from values based on the literature and from life history theory. Maximum population sizes are taken from the largest population sizes observed in the samples. Probably the greatest increase in realism in the model would come from improved information on reproduction of the prey populations, particularly reproductive time lags.

single Species, Status Quo and Multispecies Harvesting Plans

The evaluation of harvesting in the model takes place in a two step procedure. The first step is the evaluation of a static model. This static model consists of the entire model structure without long term population dynamics. This static model can be constructed from available data with a minimum of assumptions. Fish populations are fixed through a entire model run, but when a fish is harvested, the populations are changed between runs to a new fixed population size to simulate different harvesting conditions. A run of the static model is concluded when the diets of all fish species stabilize to not more than 15% change in each of three consecutive model cycles.

The second step involves evaluation of harvesting of the full model including direct harvesting and long term population dynamics. The construction of the full model requires many assumptions that are made on the basis of analogy to other fish populations. A run of the full model is concluded when all of the population sizes of all of the fish species stabilize to not more than 15% change for three consecutive model cycles. An analog of the full model is also constructed with a deterministic feeding model. This is to be used to compare the performance of stochastic and deterministic models. The four harvest strategies are: 1) no harvesting, 2) single species harvesting, 3) harvesting approximating that which is currently occurring in Southern California kelp forest recreational fishery (status quo harvesting) and 4) multispecies harvesting. These four harvesting strategies are applied to all three model structures (static, full stochastic and full deterministic).

Under the condition of no harvesting, each fish species occurs at the number of individuals corresponding to the average of all transect counts. This is the baseline from which changes in diets and populations will be measured. Comparison of these results from the static model and actual diets form the basis for the model validation.

The single species harvesting condition is one in which only the target species is taken. In this type of harvesting regime, management decisions are made as if the target species is independent of all other species. This is currently the way fisheries are managed, with a few recent exceptions (FAO 1978, Grosslien et al 1979). While in fact, no significant harvesting of these fish in these habitats occurs, there is a major hook and line recreational fishery (commercial partyboat and private boat) operating in and around coastal Southern California kelp forests on these same species. The principal target of this fishery is kelp bass, Paralabrax clathratus (Young 1969). An estimate of instantaneous mortality of approximately 0.38 for kelp bass was made by Quast (1968b) for this fishery. So in the model, the single species harvesting strategy is a fishing mortality of 0.38 for kelp bass (Table 17).

Even though one species may be the target of a fishery as kelp bass is in the Southern California recreational fishery, very few fisheries are monospecific in catch, largely because of gear selectivity is not perfect. The situation in which one species is the target of a fishery, but incidental catches of

Table 17: Instantaneous fishing mortalities for model harvesting regimes.

Species	Harvesting Regime				
	Single Species	Status Quo	Static Multi.	Stoch. Multi.	Determ. Multi.
Painted greenling					
Kelp bass	0.38	0.38	0.38	0.38	0.38
Opaleye		0.13			
Pile perch		0.02			
Black perch		0.12			
Garibaldi					
Rock wrasse (<150)					
Rock wrasse (>150)		0.01			0.38
Senorita (<150)					
Senorita (>150)		0.01			
Sheephead (<150)					
Sheephead (>150)		0.16			
Island kelpfish			0.76	0.76	0.76
Spotted kelpfish					
Blackeye goby			0.76	0.76	

other species occur is common. This is the situation in the southern California recreational fishery. In order to get some estimate of the current condition of the Southern California recreational fishery, the following procedure was used. It was assumed that fishing mortality for kelp bass in the model was 0.38 and the number of fish that would be caught at this mortality from the model population of kelp bass was calculated. Then the numbers of fish of all species used in the model that were caught in the Southern California recreational fishery was obtained by combining the commercial partyboat catch (Greenhood and Mackett 1965, Table 4) and the private boat catch (Pinkas et al. 1968, Table 22). A ratio of the model catch and the actual Southern California recreational of kelp bass was applied to the Southern California catch of the other model species. This yielded estimated model catches of these other species and these values along with the model population sizes were used to calculate rates of exploitation. These were then converted into instantaneous fishing mortality rates (Table 17). The results of this process for black perch were much too high and were arbitrarily set at a lower level. The results, except for black perch, are roughly comparable to differences in the 1964 Southern California recreational catch.

Any discussion of multispecies harvesting would have to begin with the question: What are the goals of the multispecies harvesting plan? In a model study, the answer to this question is relatively simple. However, in a true multispecies situation, the answer will probably be quite complex and could change radically depending on the point of view of the different user

groups. In this modeling exercise, the goal is to increase the diet quality of kelp bass in the static model and the catch of kelp bass in the full models. In a survey of Southern California commercial partyboat operators (Young 1969), kelp bass was rated as the second most important sport fish only after barracuda (Sphyraena argentea), a pelagic species which does not occur in these habitats. While some other species in this community are kept when caught, no other species is the object of a serious fishing effort. In view of the priorities of this fishery, the maximumizing of diet quality and catch of kelp bass is the most realistic multispecies goal.

Trophic relationships can have multispecies impacts among species three ways. The first is where one fish species directly preys on other members of the fish community. In this way, trophic relationships can have the strongest impact between species. However this mechanism does not operate in this species complex. The relatively small amount of piscivory that occurs in this community is almost exclusively directed toward juveniles of a planktivorous species, the blacksmith (Chromis punctipinnis).

The second mechanism through which trophic relationships can impact other species is through direct or interference competition. This is where one species actively excludes another from food resources, affecting the excluded species' reproduction. Again this mechanism is not important in this model.

The final mechanism for multispecies impact through trophic relations is indirect or exploitation competition. Here the

availability of food resources that are jointly used increases or decreases through feeding activity of the different species of the fish community and these changes in relative availability of food resources positively or negatively affect the species' reproduction. This is the way fish species impact each other in this community (and in the model). It is by influencing these relationships that multispecies harvesting conditions must operate to be successful.

The problem then involved with multispecies harvesting is how to release these trophic resources (or prey groups) in order to increase the appropriate optimization criteria, that is diet quality of the target species in the static model and catch in the full model. This problem can be further broken down into two parts: 1) a measure of impact through the release of prey groups on the target species by harvesting of another species and 2) the combination of species to be harvested that will provide the "best" multispecies harvesting strategy. The question of the impact of harvesting other than the target species is to find a measure of the total amount of trophic resources that will be released. For any one prey group that a potential harvested species consumes, the total amount of that resource that will be released is the amount consumed per fish times the number of fish. Since it is the impact on the target species that is of concern, these amounts are multiplied times the selectivity of that prey groups by the target species. This measure of impact of the release of prey group is the criteria for the static model. For the full model, this measure of impact is extended to reproduction of the target species and this criteria is used.

The second question is how to select the "best" combination of species to harvest under a multispecies plan. One obvious possibility is to try all possible combinations of harvesting strategies and while it would certainly yield the best solution, there are a number of problems. The first is that it is enormously wasteful in time, effort and computer costs. The second problem is that it would include a large number of possibilities that if given any consideration could be immediately rejected as impossible. The most serious problem is that this method would have no counterpart in a real situation. Clearly there must be some selection process that could shorten this task with no loss of precision and also have a counterpart in a real situation.

The alternative approach to finding the "best" combination of species to harvest is a stepwise one. In this approach, all of the species are examined to see which species would provide the largest increase in the optimization criteria for the target species. When that species is selected, the level of fishing mortality is determined from an initial estimate based on the size of the optimization criteria and then refined. The procedure then repeats itself with a new examination, selection and determination of fishing mortality. While this is a relatively simple procedure in a modeling study, in a real situation the re-examination after the addition of each species may be a problem. In these cases, species would could be inserted into the equation based on the original evaluation. This procedure can have problems since it makes no allowance for changes in the

harvesting situation due to the previous addition of species.

The final problem is when to stop the addition of species to the solution. One possible solution to this problem that does maximize optimization criteria is to completely eliminate all other species except the target species. This solution has obvious problems particularly in any attempt to use it in a real situation. So a stopping rule was chosen when the addition of a newly harvested species failed to increase the optimization criteria by 5 percent.

This procedure is used for the development of multispecies harvesting plans for all three model structures. For the static model, the starting point for the multispecies harvesting plan is single species harvesting where only the target species, kelp bass, was harvested. In order to keep the results as comparable as possible, harvesting of the target species remain fixed at the same fishing mortality (0.38) throughout all harvesting regimes. For the static model, the criteria for selecting the "best" next species to harvest in a multispecies plan is the total value of trophic resources made available to the target species by that harvesting. For each prey resource, this value is the combination of the amount of prey resource consumed by the predator, the number of predators and the selectivity of that trophic resource to the target species. These values are summed over all prey resources (Table 18). They show that harvesting of island kelpfish would have the highest impact on the target species, kelp bass. The initial level of fishing mortality of double that of the target species was selected and a sensitivity analysis of this exact value was performed. The exact value

Table 18: Optimization criteria (increase in diet quality for kelp bass) for developing a static model multispecies harvesting regime.

Species	Steps of Plan Development*		
	1	2	3
Painted greenling	97.02	156.63	150.88
Opaleye	13.42	70.44	107.55
Pile perch	0.30	0.41	0.45
Black perch	69.05	112.79	117.71
Garibaldi	20.30	119.88	109.71
Rock wrasse (<150)	48.58	93.38	94.57
Rock wrasse (>150)	302.78	557.57	606.04
Senorita (<150)	178.65	214.60	192.63
Senorita (>150)	49.85	58.03	64.45
Sheephead (<150)	59.91	148.47	159.30
Sheephead (>150)	304.92	743.59	960.34
Island kelpfish	850.67	625.35	679.53
Spotted kelpfish	10.08	7.94	21.38
Blackeye goby	387.87	759.28	393.57

* Harvesting Runs

1 = Kelp bass $F = 0.38$.

2 = Kelp bass $F = 0.38$, Island kelpfish $F = 0.70$.

3 = Kelp bass $F = 0.38$, Island kelpfish and Blackeye goby $F = 0.70$.

seems relatively unimportant since the model was unresponsive to a fairly large range of differences. One point that is made here is that since harvesting on a target species is releasing the diet of the target species, harvesting of nontarget species usually must be of much greater magnitude than that of target species to have any impact on the target species. At this point, the harvesting plan is a fishing mortality of 0.38 for the target species, kelp bass, and a fishing mortality of 0.76 for the island kelpfish. This resulted in an increase of diet quality of the target species to 9.05, an increase of 24%. The criteria for the "best" next species to add to the harvesting plan are recalculated and the "best" species to harvest is the blackeye goby (Table 18). The appropriate level of fishing mortality is determined and the new multispecies plan of a fishing mortality of 0.38 for the target species, kelp bass and a fishing mortality of 0.76 for the island kelpfish and the blackeye goby is used in a series of runs. This harvesting increased the diet quality of target species to 9.86, an increase of 9%. In the next iteration, the selection criteria (Table 18) indicate that large size class sheephead would be the next "best" species for harvesting. The result of this harvesting is that diet quality of the target species is essentially the same as in the previous iteration (9.91), ending the stepwise procedure. The final multispecies harvesting plan is a fishing mortality of 0.38 on kelp bass, the target species and a fishing mortality of 0.76 on island kelpfish and blackeye goby (Table 17). A search of other possible combinations of harvested species found no higher value of diet quality for the target species.

For the stochastic model, the construction of a multispecies harvesting plan began with the results from the single species harvesting regime which had an average yearly catch of kelp bass of 0.147 individuals/year. Using these results, the increase in population size and catch of kelp bass was calculated under the condition that the entire diet of each of the other species was transferred to kelp bass. The largest increase in catch would come from harvesting island kelpfish (Table 19) at a multiple of twice that of kelp bass harvesting, $F=0.76$. The average yearly catch of kelp bass from this harvesting was 0.160 individuals/year, an increase of 8.8% over the catch from single species harvesting. The calculations for increased population size and catch of kelp bass were made again (Table 19) and the blackeye goby was added to the multispecies harvesting plan, also at a multiple of twice that of kelp bass harvesting, $F=0.76$. The average yearly catch of kelp bass from this second step of multispecies harvesting was 0.168 individuals which was an increase of 14.3% over single species harvesting and an increase of 5.0% over the first step of multispecies harvesting. The third step showed that large rock wrasse was the next species to be added to multispecies harvesting (Table 19), again at a multiple of twice that of kelp bass harvesting $F = 0.76$. Average yearly catch from this third step of multispecies harvesting was only 0.169 individuals, only a 0.6% increase over the second step harvesting. Because of the minimum 5% increase stopping rule, the final multispecies harvesting plan was a fishing mortality of 0.38 on kelp bass and of 0.76 on island kelpfish and blackeye goby (Table 17).

Table 19: Optimization criteria (increase in kelp bass catch) for developing a stochastic model multispecies harvesting regime.

Steps of Plan Development*

Species	1	2	3
Painted greenling	0.048	0.070	0.062
Opaleye	0.014	0.021	0.019
Pile perch	0.	0.	0.001
Black perch	0.051	0.073	0.067
Garibaldi	0.024	0.035	0.036
Rock wrasse (sm.)	0.037	0.054	0.059
Rock wrasse (lg.)	0.154	0.177	0.202
Senorita (sm.)	0.088	0.118	0.112
Senorita (lg.)	0.089	0.123	0.108
Sheephead (sm.)	0.032	0.051	0.053
Sheephead (lg.)	0.056	0.081	0.081
Island kelpfish	0.170	0.094	0.101
Spotted kelpfish	0.004	0.005	0.005
Blackeye goby	0.113	0.180	0.072

* Harvesting Runs

1 = Kelp bass $F = 0.38$.

2 = Kelp bass $F = 0.38$, Island kelpfish $F = 0.70$.

3 = Kelp bass $F = 0.38$, Island kelpfish and Blackeye goby $F = 0.70$.

For developing a multispecies harvesting plan for the deterministic model, single species harvesting from this model was again the starting point. Increased population sizes and catches were the outcome of a shift of the entire diet of each species to kelp bass. The order of species added to the multispecies harvesting plan was different than those used in the stochastic model. Large rock wrasse was the first fish to be added to the multispecies harvesting plan (Table 20) at one multiple of the kelp bass harvesting, $F=0.38$. This increased kelp bass catch from 0.191 individuals/year to 0.225 individuals/year, an 18% increase. Runs were made in which large rock wrasse was harvested at twice the rate imposed on kelp bass, $F=0.76$ which resulted in a slight decrease in the catch rate of kelp bass. Another iteration of the calculations were performed and the harvesting of blackeye goby would make the next "best" contribution (Table 20). This was added to the multispecies harvesting plan at a multiple of twice the harvesting of kelp bass ($F=0.76$). The increased catch level of kelp bass from this harvesting strategy was 0.242 individuals/year, a 7.6 percent increase. The next iteration showed that island kelpfish would make the next "best" contribution and it was added to the harvesting plan (Table 20). This run had a catch of 0.236 individuals/year, a decrease of two percent and so the multispecies harvesting was stopped due to the 5% stopping rule at the previous cycle with large rock wrasse and blackeye goby (Table 17).

Table 20: Optimization criteria (increase in kelp bass catch) for developing a deterministic model multispecies harvesting regime.

Species	Steps of Plan Development*		
	1	2	3
Painted greenling	0.034	0.058	0.088
Opaleye	0.044	0.086	0.127
Pile perch	0.005	0.006	0.007
Black perch	0.067	0.096	0.145
Garibaldi	0.019	0.029	0.044
Rock wrasse (sm.)	0.039	0.054	0.081
Rock wrasse (lg.)	0.240	0.156	0.232
Senorita (sm.)	0.138	0.111	0.169
Senorita (lg.)	0.090	0.159	0.238
Sheephead (sm.)	0.042	0.056	0.085
Sheephead (lg.)	0.056	0.083	0.126
Island kelpfish	0.105	0.174	0.265
Spotted kelpfish	0.002	0.003	0.003
Blackeye goby	0.191	0.270	0.147

* Harvesting runs.

1 = Kelp bass $F=0.38$.

2 = Kelp bass, Rock wrasse $F=0.38$.

3 = Kelp bass, Rock wrasse $F=0.38$, Blackeye goby $F=0.76$.

MODEL VALIDATION

The purpose of model validation is "to prove the model to be true" (Naylor and Finger 1971); however, procedures to accomplish this are only vaguely defined. Validation procedures usually center around whether the model is behaving in a "reasonable" manner. In serious attempts at model validation, the question of "reasonable" behavior usually takes the form of one of three questions (Naylor and Finger 1971). The first is, to what degree does model behavior conform to existing and relevant theory? In this case, the model was directly derived from optimal foraging theory, and the results closely parallel theoretical expectations. The second question is, to what degree does the model accurately forecast future states of the system? This is probably the best method of model validation. One attempt was made toward a species removal experiment but because of extreme oceanographic events, the experiment was disrupted. The third question is, to what degree does the model behavior duplicate past system behavior? There is commonly some circularity in this approach to validation, since the same set of data is used both to estimate parameters and as criteria of model performance. This is minimized to some degree by using selectivity coefficients that are estimated from diets and prey environments from a series of distinctly different habitats while the model estimates overall population diets from a different prey environment.

For this part of the validation, the actual values of the

fishes' diet were compared to the no harvesting results of the static model. The two sets of diet values were expanded back to the average gut volume of that species and were compared with a Chi-square goodness of fit test. Of the fifteen species, six (kelp bass, black perch, small and large sheephead, island kelpfish and spotted kelpfish), have significant differences between the two sets of values at the 5% level (Table 19). For four of these species (black perch, small sheephead, island kelpfish and spotted kelpfish), the dropping of one rare (less than 0.1% of the diet volume of the actual values) prey category would have reduced the probability to less than 50%. The differences in the remaining two species kelp bass and large sheephead is due to lack of natantian decapods in the model results. This trend is evident in other fish species diets but not at this significant a level. This problem stems from the estimation of parameters and could have been caused by one of three problems: 1) a higher estimate of these decapods in the gut diet volume due to differential digestion, 2) a lower estimate of the decapods in the prey environment due to their mobility and evasiveness or 3) a nonuniform selectivity in which predators after they have reached a certain level of gut fullness will take only certain highly preferred prey. This is the situation that Ivlev (1961) found in experimental feeding trials. The answer is probably some combination of the last two. Except for these two species, the fit of the actual and simulated results is quite good and the results of this validation are sufficient to warrant a high degree of confidence in the model results.

Table 21: Model validation Chi-square values for tests between actual diet and no harvesting model runs.

Species	Chi-square values	d.f.	Prob.
Painted greenling	10.66	17	0.87
Kelp bass	76.92	16	0.01
Opaleye	16.95	10	0.08
Pile perch	4.37	6	0.63
Black perch	44.88	23	0.03
Garibaldi	15.25	21	0.81
Rock wrasse (<150)	8.86	18	0.96
Rock wrasse (>150)	15.21	26	0.95
Senorita (<150)	5.67	26	0.98
Senorita (>150)	25.09	20	0.20
Sheephead (<150)	86.70	16	0.01
Sheephead (>150)	114.66	25	0.01
Island kelpfish	24.71	13	0.04
Spotted kelpfish	35.68	14	0.01
Blackeye goby	25.70	24	0.38

MODEL RESULTS

static Model

The results of single species and status quo harvesting regimes are virtually identical in terms of management goals (in the static model, increasing diet quality of kelp bass) (Table 22). The harvesting of opaleye, black perch and large sheephead had virtually no impact in increasing dietary quality of kelp bass. These two harvesting regimes both had increased diet quality from the no harvesting regime. This is a result of the harvesting of kelp bass and the corresponding release of prey resources. The release of prey resources allowed a shift in the diet of kelp bass to higher selectivity prey and hence a higher diet quality overall.

The impact of multispecies harvesting on diet quality, given the condition that fish population sizes are constant, can be analyzed by dividing the fifteen species into three different groups: 1) species whose diet improve in quality (dietary winners), 2) species whose diet decline in quality (dietary losers), and 3) species whose diets quality remain unchanged (dietary neutrals). The first group, dietary winners, is made up of kelp bass (Table 22), island kelpfish (Table 23), blackeye goby (Table 24) and smaller rock wrasse (Table 25). Increases in dietary quality range from 15 to 160 per cent. Strong shifts in diet are exhibited by all these species. These shifts are characterized by increases in dietary volume of reptantia and natantia decapods and to a much lesser degree in some species, by

Table 22. Diet volume of prey in percent by taxonomic group for the diet of kelp bass, Paralabrax clathratus, from stomach contents and from the static model for the four harvesting regimes.

	Harvesting Regime				
	Stomach Contents	No Harves-ting	Single Spec.	Status Quo	Multi Spec.
Fish	4.71	5.98	10.39	6.10	16.07
Fish eggs	1.32	0.16	0.12	0.09	0.02
Algae	0.15	0.14	0.08	0.14	0.01
Hydrozoa	0.59	1.67	1.27	1.18	0.16
Polychaeta	4.83	5.83	4.95	4.94	0.72
Ostracoda	0.15	1.58	1.32	1.33	0.16
Calanoida	0.60	0.52	0.45	0.43	0.05
Harpacticoida	0.29	3.40	2.88	2.86	0.37
Mysidacea	8.30	8.10	8.74	8.87	1.33
Cumacea	0.44	0.33	0.35	0.31	0.03
Tanaidacea	3.62	8.97	7.62	7.56	0.95
Isopoda	2.67	11.11	9.36	9.14	1.34
Gammaridea	12.93	23.38	20.06	19.75	2.73
Caprellidea	14.39	24.53	21.55	21.58	3.38
Reptantia	7.91	1.18	0.81	0.71	38.37
Natantia	37.43	2.94	9.72	14.67	34.29
Ophiuroidea	0.09	0.18	0.34	0.34	0.02
Diet quality	11.25	6.74	7.30	7.55	9.86

Table 23. Diet volume of prey in percent by taxonomic group for the diet of island kelpfish, Alloclinus holderi, from stomach contents and from the static model for the four harvesting regimes.

	Stomach Contents	Harvesting Regime			
		No Harves- -ting	Single Spec.	Status Quo	Multi Spec.
Fish eggs	1.39	0.17	0.15	0.14	0.02
Polychaeta	3.44	2.16	1.93	2.28	0.28
Gastropoda	1.78	1.23	0.86	1.20	0.12
Veleger	0.06	0.05	0.14	0.02	0.
Bivalvia	0.11	0.44	0.39	0.30	0.03
Ostracoda	0.29	0.08	0.06	0.07	0.01
Harpacticoida	0.06	0.11	0.09	0.10	0.01
Mysidacea	0.28	0.42	0.42	0.48	0.04
Cumacea	0.08	2.37	2.25	2.19	0.18
Isopoda	10.56	13.99	12.05	13.34	1.10
Gammaridea	29.59	42.89	36.14	38.96	3.18
Caprellidea	20.17	23.88	20.43	21.93	2.01
Reptantia	7.33	5.94	4.95	4.12	68.00
Natantia	25.22	6.29	20.14	14.86	25.03
Diet quality	15.23	11.24	13.56	12.38	31.76

Table 24. Diet volume of prey in percent by taxonomic group for the diet of the blackeye goby, Coryphopterus nicholsii, from stomach contents and from the static model for the four harvesting regimes.

	Stomach Contents	Harvesting Regime			
		No Harves -ting	Single Spec.	Status Quo	Multi Spec.
Fish	1.11	0.01	0.01	0.01	0.59
Fish eggs	0.61	0.01	0.01	0.01	0.
Algae	0.66	5.88	4.21	4.78	1.43
Foraminifera	0.45	0.44	0.41	0.37	0.15
Porifera	0.26	0.21	0.13	0.22	0.07
Nemertea	0.26	0.03	0.04	0.04	0.01
Polychaeta	14.43	19.82	18.60	17.53	6.50
Polyplacophora	0.66	0.65	0.15	0.15	0.13
Gastropoda	9.54	14.43	13.27	12.99	5.91
Bivalvia	7.80	2.02	2.39	2.22	0.89
Pycnogonida	1.22	1.24	1.05	1.32	0.46
Ostracoda	5.69	0.26	0.25	0.23	0.09
Calanoida	0.69	9.19	8.66	7.99	2.99
Harpacticoida	1.50	0.15	0.12	0.11	0.04
Cyclopoida	2.32	0.40	0.38	0.36	0.13
Cumacea	3.38	5.26	4.84	4.49	1.60
Tanaidacea	0.82	4.03	3.80	3.52	1.36
Isopoda	2.83	6.62	6.38	5.84	2.23
Gammaridea	15.67	14.87	14.54	13.41	5.13
Caprellidea	2.80	2.81	2.68	2.47	0.93
Reptantia	2.51	1.40	2.20	1.32	35.12
Natantia	2.51	5.40	12.01	15.81	31.32
Bryozoa	7.11	0.21	0.34	0.20	0.15
Ophiuroidea	14.08	4.03	3.30	4.15	1.71
Echinoidea	1.31	0.80	0.25	0.50	1.03
Diet quality	4.56	5.58	5.94	6.16	6.42

Table 25. Diet volume of prey in percent by taxonomic groups for the diet of smaller (>150 mm) rock wrasse, Halichoeres semicinctus, from stomach contents and from the static model for the four harvesting regimes.

	Stomach Contents	Harvesting Regime			
		No Harves -ting	Single Spec.	Status Quo	Multi Spec.
Fish eggs	0.46	0.01	0.	0.04	0.
Algae	0.84	0.31	0.14	0.58	0.17
Hydrozoa	0.01	0.72	1.24	0.28	0.37
Polychaeta	6.92	7.84	7.85	5.61	1.32
Gastropoda	16.42	9.47	7.89	8.58	1.97
Bivalvia	3.79	6.09	5.89	5.61	1.18
Pycnogonida	0.28	0.01	0.	0.	0.
Ostracoda	0.29	1.81	1.45	1.60	0.38
Cirripedia	0.46	0.10	0.	0.	0.02
Cumacea	0.92	0.33	0.20	0.26	0.04
Tanaidacea	2.03	0.34	0.31	0.32	0.09
Isopoda	0.55	5.72	4.55	5.62	1.36
Gammaridea	42.02	27.71	23.86	24.86	6.22
Caprellidea	6.55	8.99	7.52	7.67	1.82
Reptantia	1.84	4.37	4.09	2.46	58.89
Natantia	1.00	2.72	12.72	13.24	18.51
Bryozoa	15.41	13.66	13.69	14.10	5.55
Ophiuroidea	4.34	7.30	5.92	6.38	1.47
Ascidacea	2.31	2.51	2.69	2.80	0.63
Diet quality	6.36	6.84	7.28	7.29	9.63

fish. The corresponding decrease in dietary volume are due to a decline in dietary importance of gammarid and caprellid amphipods, isopods, polychaetes and mollusks. Prey groups which decline in dietary importance were unique to each particular fish species. Increases in dietary quality of dietary winners are caused by the replacement in the diet of lower selectivity prey by those of higher selectivity. Decapods were prey with either the highest or among the highest selectivity values for dietary winners; and increases in dietary quality resulted from greater incorporation of these prey. Dietary winners are, by and large, the fish species that are harvested in the multispecies harvesting regime.

The second group, dietary losers, is made up of painted greenling (Table 26), opaleye (Table 27), black perch (Table 28), Garibaldi (Table 29), larger rock wrasse (Table 30), smaller and larger sheephead (Tables 31&32), and spotted kelpfish (table 33). Their shifts in diet are less dramatically influenced by the multispecies harvesting regime than the dietary winners. Both in terms of change in dietary volumes that shifted from one prey to another and in the degree of change of dietary quality. As with dietary winners, this group had increases in the dietary volumes of reptantia and natantia decapods and in some species, fish. For dietary losers, prey groups which decrease in importance are, for the most part, unique to a specific species of fish. Selectivity for natantia and reptantia decapods are in the high to intermediate range for these fish species. They are of lower selectivity than the prey groups they replace but are taken at

Table 26. Diet volume of prey in percent by taxonomic group for the diet of painted greenling, Oxylebius pictus, from stomach contents and from the static model for the four harvesting regimes.

	Harvesting Regime				
	Stomach Contents	No Harves -ting	Single Spec.	Status Quo	Multi Spec.
Fish	2.56	2.06	3.23	3.87	17.03
Fish eggs	1.28	0.11	0.07	0.11	0.03
Fish larva	1.23	1.37	1.28	0.64	0.53
Algae	0.15	0.04	0.07	0.	0.06
Hydrozoa	0.74	4.00	4.24	4.43	1.12
Polchaeta	1.92	6.19	4.87	5.01	1.74
Gastropoda	0.10	1.20	1.08	1.03	0.27
Bivalvia	0.98	0.34	0.38	0.34	0.10
Pycnogonida	0.10	0.37	0.40	0.35	0.08
Ostracoda	0.10	0.03	0.03	0.03	0.01
Cirripedia	0.49	3.58	3.62	3.36	1.15
Tanaidacea	0.15	0.20	0.11	0.08	0.03
Isopoda	7.74	14.49	14.06	13.82	4.64
Gammaridea	45.44	37.81	37.31	37.15	11.88
Caprellida	20.43	23.70	23.24	22.95	7.17
Reptantia	7.73	3.79	1.58	1.18	41.99
Natantia	8.76	0.78	4.42	5.63	12.14
Bryozoa	0.10	0.04	0.02	0.03	0.02
Diet quality	11.86	12.68	12.51	12.47	8.57

Table 27. Diet volume of prey in percent by taxonomic group for the diet of opaleye, Girella nigricans, from stomach contents and from the static model for the four harvesting regimes.

	Harvesting Regime				
	Stomach Contents	No Harves- -ting	Single Spec.	Status Quo	Multi Spec.
Algae	75.53	69.85	71.88	70.77	40.55
Hydrozoa	15.25	6.61	6.82	7.55	4.24
Gastropoda	0.96	1.13	1.49	1.49	0.41
Ostracoda	0.07	0.20	0.20	0.17	0.11
Harpacticoida	0.04	0.78	0.73	0.72	0.42
Cyclopoida	0.01	0.01	0.	0.01	0.
Isopoda	0.35	7.46	7.39	6.81	3.86
Gammaridea	4.90	7.11	6.61	6.55	4.00
Caprellidae	0.21	0.31	0.24	0.20	0.18
Reptantia	2.15	3.17	1.19	1.79	43.79
Bryozoa	0.53	3.36	3.44	3.94	2.43
Diet quality	33.52	28.75	29.49	29.36	18.27

Table 28. Diet volume of prey in percent by taxonomic group for the diet of black perch, Embiotoca jackonsi, from stomach contents and from the static model for the four harvesting regimes.

	Stomach Contents	Harvesting Regime			
		No Harves-ting	Single Spec.	Status Quo	Multi Spec.
Algae	1.68	0.91	0.92	0.79	0.70
Foraminifera	0.19	0.29	0.23	0.31	0.14
Porifera	0.01	0.02	0.	0.02	0.01
Hydrozoa	0.07	4.81	4.75	4.60	2.48
Polychaeta	7.50	5.64	4.94	5.54	3.48
Polyplacophora	0.01	0.01	0.	0.01	0.
Gastropoda	2.19	9.45	9.78	8.85	5.43
Bivalvia	1.22	1.33	1.11	1.27	0.67
Ostracoda	0.03	0.15	0.13	0.14	0.08
Harpacticoida	0.03	0.02	0.01	0.01	0.01
Cyclopoida	0.01	0.07	0.05	0.07	0.02
Mysidacea	0.07	0.42	0.53	0.45	0.28
Cumacea	0.01	1.35	1.22	1.19	0.66
Tanaidacea	2.38	5.74	4.60	4.91	2.91
Isopoda	3.25	4.66	3.95	4.34	2.62
Gammaridea	54.86	47.13	40.99	44.06	25.78
Caprellidae	2.62	7.67	6.55	7.48	3.94
Reptantia	2.63	1.43	2.78	2.78	29.08
Natantia	3.96	0.92	7.79	4.76	15.24
Bryozoa	3.06	0.75	0.82	0.97	0.49
Ophiuroidea	6.88	2.68	4.45	3.67	2.70
Echinoidea	0.35	1.69	0.79	0.40	1.30
Ascidacea	5.64	3.28	3.59	3.39	2.00
Entoprocta	0.01	0.01	0.01	0.01	0.01
Diet quality	5.64	6.93	6.60	6.68	5.14

Table 29. Diet volume of prey in percent by taxonomic group for the diet of Garibaldi, Hypsypops rubicundus, from stomach contents and from the static model for the four harvesting regimes.

	Harvesting Regime				
	Stomach Contents	No Harves- -ting	Single Spec.	Status Quo	Multi Spec.
Fish	0.58	2.74	3.94	3.95	6.34
Algae	49.32	41.88	42.25	41.80	18.64
Foraminifera	1.65	0.35	0.38	0.34	0.15
Porifera	0.38	0.25	0.29	0.36	0.25
Hydrozoa	5.60	4.27	2.72	3.05	1.43
Anthozoa	3.36	1.77	1.88	2.33	0.83
Polychaeta	1.92	2.09	2.10	1.80	0.81
Gastropoda	0.96	3.39	2.49	3.26	1.23
Bivalvia	0.19	0.82	0.72	0.50	0.35
Cephalopoda	0.19	0.01	0.01	0.01	0.01
Ostracoda	0.05	0.04	0.05	0.04	0.02
Harpacticoida	0.02	0.03	0.03	0.03	0.02
Cirripedia	0.50	3.75	3.63	3.33	1.57
Tanaidacea	0.01	0.01	0.01	0.01	0.01
Isopoda	0.02	0.06	0.08	0.04	0.02
Gammaridea	20.83	10.86	10.81	10.43	4.09
Caprellidae	0.32	0.11	0.06	0.08	0.07
Reptantia	0.19	5.86	4.82	3.22	53.03
Bryozoa	20.09	13.60	15.05	16.01	7.35
Asteroidea	3.84	3.72	4.32	4.14	1.36
Ophiuroidea	0.29	0.70	0.22	0.45	0.36
Asciacea	7.97	3.90	4.14	4.85	2.09
Diet quality	16.16	13.32	13.19	13.16	8.96

Table 30. Diet volume of prey in percent by taxonomic group for the diet of larger (>150 mm) Halichoeres semicinctus, from stomach contents and from the static model for the four harvesting regimes.

	Stomach Contents	Harvesting Regime			
		No Harves -ting	Single Spec.	Status Quo	Multi Spec.
Fish eggs	1.10	0.09	0.18	0.12	0.06
Algae	4.78	8.06	7.92	7.46	3.83
Foraminifera	0.06	0.07	0.06	0.06	0.03
Porifera	0.06	0.96	0.77	0.74	0.37
Hydrozoa	0.15	0.11	0.11	0.21	0.09
Nemertea	0.05	0.25	0.23	0.27	0.11
Polychaeta	11.41	5.49	5.35	5.31	3.25
Polyplacophora	0.03	0.42	0.13	0.27	0.22
Gastropoda	7.08	11.89	11.36	12.29	4.85
Bivalvia	5.56	5.92	5.67	5.66	2.19
Pycnogonida	0.25	0.51	0.39	0.43	0.20
Ostracoda	0.52	0.01	0.01	0.02	0.01
Harpacticoida	0.05	0.85	0.75	0.75	0.34
Cirripedia	0.32	0.52	0.35	0.54	0.19
Mysidacea	0.12	0.24	0.20	0.19	0.07
Cumacea	0.06	0.25	0.25	0.26	0.08
Tanaidacea	0.28	2.01	1.86	1.87	0.83
Isopoda	3.34	5.52	4.88	4.89	2.14
Gammaridea	17.01	17.49	16.45	16.29	7.27
Caprellidae	5.88	20.24	19.13	18.72	8.07
Reptantia	9.13	2.04	1.92	1.54	41.68
Natantia	1.43	1.27	4.29	5.24	15.43
Bryozoa	14.43	7.61	8.85	8.81	5.02
Asteroidae	0.18	0.38	0.98	0.27	0.07
Ophuroidea	10.46	4.99	5.33	4.80	1.86
Echinoidea	1.03	0.47	0.44	0.88	0.73
Ascidacea	5.28	2.32	2.13	2.10	0.99
Diet quality	4.90	5.49	5.47	5.46	4.66

Table 31. Diet volume of prey in percent by taxonomic group for the diet of smaller (<150 mm) sheephead, Semicossyphus pulcher, from stomach contents and from the static model for the four harvesting regimes.

	Stomach Contents	Harvesting Regime			
		No Harves -ting	Single Spec.	Status Quo	Multi Spec.
Fish eggs	1.71	0.14	0.44	0.13	0.03
Nemertea	2.14	0.74	0.61	0.68	0.16
Polychaeta	14.29	20.35	21.42	18.28	5.85
Polyplacophora	0.14	0.21	0.	0.	0.16
Gastropoda	1.60	11.64	12.06	12.25	2.85
Bivalvia	13.14	9.36	8.07	7.73	2.72
Ostracoda	0.74	0.97	0.87	0.81	0.26
Cyclopoida	0.01	3.28	3.06	3.14	1.06
Caligoida	0.15	0.01	0.	0.	0.
Tanaidacea	0.71	2.24	2.16	2.10	0.66
Isopoda	2.44	7.11	6.66	6.89	2.07
Gammaridea	47.14	34.72	32.31	31.97	10.11
Caprellidea	1.49	0.91	0.84	0.75	0.25
Reptantia	5.36	4.86	1.14	2.84	57.28
Natantia	6.28	0.76	6.37	7.78	14.01
Ophiuroidea	0.71	2.36	1.74	2.37	1.18
Echinoidea	1.71	0.35	2.60	2.27	1.34
Diet quality	6.28	6.28	6.56	6.38	5.91

Table 32. Diet volume of prey in percent by taxonomic group for the diet of larger (>150 mm) sheephead, Semicossyphus pulcher, from stomach contents and from the static model for the four harvesting regimes.

	Harvesting Regime				
	Stomach Contents	No Harves-ting	Single Spec.	Status Quo	Multi Spec.
Fish	0.96	5.54	8.09	8.42	28.17
Algae	1.84	2.71	2.64	2.61	0.79
Foraminifera	0.01	0.10	0.06	0.08	0.02
Porifera	2.71	0.37	0.49	0.38	0.11
Hydrozoa	0.01	0.19	0.33	0.25	0.01
Anthozoa	0.11	3.73	3.77	3.57	1.15
Nemertea	0.01	0.01	0.01	0.01	0.
Polychaeta	11.32	17.74	16.22	16.23	5.34
Polyplacophora	0.41	0.44	0.55	0.82	0.11
Gastropoda	8.37	28.96	26.35	26.91	6.76
Bivalvia	23.52	11.52	10.97	10.57	2.90
Pycnogonida	0.32	0.51	0.52	0.57	0.02
Ostracoda	0.07	0.01	0.01	0.01	0.01
Cirripedia	1.62	8.84	8.09	8.30	2.31
Cumacea	0.06	0.07	0.02	0.03	0.01
Tanaidacea	0.30	0.04	0.04	0.04	0.01
Isopoda	1.93	2.25	2.26	2.06	0.58
Gammaridea	6.69	5.82	5.15	5.31	1.56
Caprellidea	0.25	3.37	3.12	3.14	0.84
Reptantia	20.86	1.69	2.57	2.14	37.76
Natantia	4.82	1.97	4.68	4.43	9.68
Bryozoa	4.87	1.54	1.68	1.69	0.66
Ophiuroidea	1.45	1.41	1.27	1.38	0.55
Echinoidea	5.46	0.36	0.45	0.56	0.47
Holothuroidea	0.03	0.	0.01	0.	0.
Asciadiacea	1.95	0.81	0.68	0.46	0.17
Diet quality	8.15	7.91	7.62	7.58	5.51

Table 33 Diet volume of prey in percent by taxonomic group for the diet of spotted kelpfish, Gibbonsia elegans, from the static model for the four harvesting regimes.

	Harvesting Regime				
	Stomach Contents	No Harves-ting	Single Spec.	Status Quo	Multi Spec.
Fish	0.31	0.52	0.	0.82	1.88
Fish eggs	0.40	0.01	0.01	0.	0.01
Algae	0.32	1.92	2.12	2.06	0.68
Foraminifera	0.40	0.74	0.71	0.69	0.26
Polychaeta	0.63	3.52	3.30	2.66	1.53
Gastropoda	1.27	2.33	2.01	2.29	0.62
Cladocera	0.32	0.01	0.01	0.01	0.01
Ostracoda	0.24	0.02	0.01	0.02	0.01
Calanoida	0.24	0.11	0.08	0.11	0.03
Cirripedia	0.01	0.06	0.08	0.04	0.01
Isopoda	18.22	28.12	27.21	27.66	10.52
Gammaridea	50.00	51.51	48.93	49.11	18.92
Caprellidea	4.91	8.94	7.63	7.91	3.07
Reptantia	8.64	1.28	0.60	1.51	48.00
Natantia	14.42	1.60	7.30	5.43	15.52
Diet quality	13.02	14.50	14.39	14.41	11.83

higher rates because of increased availability due to the multispecies harvesting. The result is lower diet quality for the dietary losers.

The three fishes: pile perch (Table 34), smaller and larger seniorita (Tables 35&36), which exhibit no significant change in diet quality under multispecies harvesting, are all species which either a very low or zero selectivity for the two decapod prey groups. These fish are trophically isolated from the rest of the fish community. Pile perch is a specialized mollusk feeder with heavy pharyngeal teeth. Its diet is principally made up of gastropods and bivalves. Although, there was some increase in gastropod availability because of dietary replacement of gastropods by decapods, primarily from larger sheephead, it had no significant impact on pile perch diet. Both smaller and larger seniorita had small non-significant increases in dietary quality. This was the result of an increase in the bryozoan population. This increased level was also caused by the replacement of bryozoans in other species' diet by decapod crustaceans.

From this, it is clear that the objective of the multispecies harvesting regime should be to increase the availability of reptantia and natantia decapods through harvesting other species which feed heavily on these prey groups. These two prey groups are both large volume prey, so therefore have a large impact on an individual feeding period and very highly selected prey for the target species: kelp bass. These two factors interact so that a very small shift in numbers of these prey in the diet can have a large impact on diet quality.

Table 34. Diet volume of prey in percent by taxonomic group for the diet of pile perch, Damalichthys vacca, from stomach contents and from the static model for the four harvesting regimes.

	Stomach Contents	Harvesting Regime			
		No Harves -ting	Single Spec.	Status Quo	Multi Spec.
Polychaeta	1.04	2.58	1.53	1.98	2.68
Gastropoda	18.96	47.98	51.14	52.24	49.54
Bivalvia	72.42	45.73	43.75	42.08	42.87
Isopoda	0.13	0.04	0.10	0.14	0.07
Gammaridea	0.39	0.54	0.50	0.60	0.47
Ophiuroidea	6.53	3.14	1.47	2.46	2.68
Echinoidea	0.52	0.01	1.50	0.50	1.69
Diet quality	46.78	35.48	35.04	34.20	34.36

Table 35. Diet volume of prey in percent by taxonomic group for the diet of smaller (>150 mm) senorita, Oxyjulis californica, from stomach contents and from the static model for the four harvesting regimes.

	Stomach Contents	Harvesting Regime			
		No Harves -ting	Single Spec.	Status Quo	Multi Spec.
Fish eggs	0.70	0.	0.	0.	0.02
Algae	9.70	12.80	12.12	10.52	10.51
Porifera	0.04	0.	0.	0.01	0.
Hydrozoa	0.20	3.17	2.25	3.04	3.42
Polychaeta	10.36	13.17	12.98	12.83	13.36
Gastropoda	0.78	1.33	1.50	0.50	1.16
Veleger	0.62	0.52	0.24	0.24	0.62
Bivalvia	0.29	1.09	0.78	1.10	0.93
Pycnogonida	3.64	0.01	0.	0.13	0.
Cladocera	4.50	0.01	0.	0.	0.
Ostracoda	0.04	0.02	0.01	0.01	0.01
Calanoida	10.73	5.03	5.00	5.08	5.14
Harpacticoida	0.01	0.02	0.04	0.04	0.04
Cyclopoida	2.54	0.11	0.09	0.10	0.10
Caligoida	3.81	0.09	0.06	0.08	0.09
Cirripedia	6.60	0.68	0.76	1.06	1.10
Tanaidacea	0.04	0.04	0.02	0.04	0.04
Isopoda	6.18	15.68	13.96	14.43	13.75
Gammaridea	17.20	12.50	12.01	11.67	11.97
Caprellidea	4.83	14.25	14.65	14.29	13.77
Euphausiacea	0.20	0.01	0.	0.09	0.
Natantia	0.01	0.	0.	0.65	1.10
Insecta	0.04	0.01	0.01	0.	0.01
Bryozoa	16.87	19.39	23.24	23.98	22.88
Ophiuroidea	0.08	0.01	0.29	0.	0.
Echinoidea	0.04	0.	0.	0.	0.
Diet quality	7.55	10.26	10.55	10.74	10.54

Table 36. Diet volume of prey in percent by taxonomic group for the diet of larger (>150 mm) senorita, Oxyjulis californica, from stomach contents and from the static model for the four harvesting regimes.

	Stomach Contents	Harvesting Regime			
		No Harves -ting	Single Spec.	Status Quo	Multi Spec.
Fish eggs	0.65	0.02	0.	0.02	0.
Algae	17.72	21.33	21.04	19.92	21.08
Polychaeta	20.46	15.94	14.44	15.72	14.08
Polyplacophora	0.06	0.35	0.33	0.33	0.
Gastropoda	6.23	10.40	9.84	10.50	10.89
Bivalvia	3.37	0.71	0.30	0.48	0.31
Cladocera	2.79	0.01	0.01	0.01	0.01
Ostracoda	0.06	0.01	0.01	0.01	0.01
Calanoida	0.35	11.69	11.47	11.87	11.96
Harpacticoida	0.88	0.10	0.10	0.08	0.07
Cyclopoida	0.06	0.34	0.34	0.37	0.35
Caligoida	0.06	0.03	0.03	0.03	0.03
Mysidacea	0.06	0.01	0.03	0.01	0.
Isopoda	3.03	2.33	2.18	1.97	1.87
Gammaridea	5.00	4.74	4.44	4.07	4.47
Caprellidea	6.34	6.41	5.75	5.30	5.23
Natantia	0.57	0.63	0.	0.59	1.50
Bryozoa	29.64	19.88	23.59	22.92	21.81
Ophiuroidea	0.41	4.52	5.28	5.28	5.36
Echinoidea	0.11	0.01	0.	0.	0.
Ascidacea	1.98	0.56	0.82	0.52	0.26
Diet quality	10.85	11.82	12.32	12.24	12.14

prey that were replaced represented a large number of prey groups having lower selectivities and smaller volumes. The multispecies harvesting regime reduced predation pressure on these high selectivity prey resulting in their increased abundance for kelp bass and other decapod feeding fishes. This general reduction in predation pressure on the two decapod groups had differing effects on different species but it increased the dietary quality of kelp bass by 40%.

A special model was constructed where kelp bass was the only fish species feeding. Dietary quality for kelp bass from this run was actually lower than from multispecies harvesting (8.67 vs 9.84). This is because foraging by other fish species reduces the abundance of prey other than the reptantia and natantia decapods and therefore increase the relative abundance of the two decapod groups. Kelp bass feeding under the condition of being the only fish species, actually encounters fewer of these highly selected prey and hence has a lower dietary quality.

The three groups of fish: dietary winners, dietary losers and dietary neutrals (or trophical isolates), are not so much independent categories of fishes but more a grouping of fishes along a continuum based on how strong their selectivity for the two decapod groups is relative to their selectivities for other prey. Dietary winners have very high selectivity values for these two groups relative to that of their overall diet. Dietary losers have much lower selectivity for these two prey groups relative to their overall diet and dietary neutrals have very low selectivity values for these prey. It is the selectivity values

of these two prey groups, natantia and reptantia decapods, in relation to those of the rest of the prey that make up the diet, that control the fish species response to the new conditions caused by harvesting. There is relatively little secondary effect in which fish diets would change due to release of prey groups due to the shift to decapods.

Stochastic Model

The addition of long term fish population dynamics into the model structure resulted in a increase in stability of the overall system. Compared to the static model, full model runs reached equilibrium in fewer numbers of cycles (No Harvesting 15 vs 19 years, Single Species 17 vs 21 years and Status Quo 17 vs 22 years), and prey populations changed less dramatically in terms of absolute high and low population values. The fish populations, of course, were constant in the static model, but were allowed to vary in the stochastic model. This increase in stability is attributed to the fact that fish populations were allowed to vary in response to changes in dietary condition. By allowing fish populations to vary, the degree of variation in other parts of the model, particularly diet, was reduced.

The response of fish species to the first three harvesting regimes: no harvesting, single species and status quo, are virtually identical except for the actual harvesting of kelp bass in the single species and status quo harvesting regimes (Table 37). All of the species which were harvested to any degree: kelp bass, opaleye, black perch and large sheephead, had small increases in diet quality which were translated into an increase in population size (Tables 37, 38, 39 and 40). This was because the model is based on trophic relationships. Any harvesting of a fish predator released some quantity of prey which otherwise would have been consumed. The predator most likely to benefit from the particular mix of prey being released was, of course, the fish that had been just harvested; so each fish being harvested responded with some degree of increase in diet quality

Table 37. Diet volume of prey in percent by taxonomic group for the diet of kelp bass, Paralabrax clathratus, from the stochastic model for the four harvesting regimes.

	Harvesting Regime			
	No Harves- -ting	Single Spec.	Status Quo	Multi Spec.
Fish	4.75	7.39	8.37	5.92
Fish eggs	0.14	0.16	0.15	0.11
Algae	0.12	0.10	0.12	0.10
Hydrozoa	1.52	1.47	1.38	1.32
Polychaeta	6.05	5.56	5.57	5.16
Ostracoda	1.68	1.54	1.52	1.36
Calanoida	0.56	0.49	0.49	0.44
Harpacticoida	3.63	3.33	3.24	2.91
Mysidacea	7.82	11.03	10.83	10.10
Cumacea	0.41	0.37	0.34	0.32
Tanaidacea	9.65	8.87	8.63	7.85
Isopoda	11.48	10.87	10.52	9.89
Gammaridea	24.40	22.54	22.18	21.05
Caprellidea	24.64	23.72	23.51	24.13
Reptantia	1.12	0.94	1.06	1.63
Natantia	1.80	1.37	1.89	7.42
Ophiuroidea	0.23	0.22	0.20	0.28
Diet quality	6.64	6.77	6.79	7.52
Pop. size	0.67	0.47	0.47	0.56
Catch	-	0.15	0.15	0.17

Table 38. Diet volume of prey in percent by taxonomic group for the diet of opaleye, Girella nigricans, from the stochastic model for the four harvesting regimes.

	Harvesting Regime			
	No Harves- -ting	Single Spec.	Status Quo	Multi Spec.
Algae	73.60	72.75	72.60	71.94
Hydrozoa	7.09	7.51	7.06	7.73
Gastropoda	1.89	1.49	1.97	1.22
Ostracoda	0.19	0.21	0.20	0.18
Harpacticoida	0.80	0.81	0.77	0.75
Cyclopoida	0.01	0.02	-	0.01
Isopoda	7.61	7.48	7.39	7.38
Gammaridea	7.02	7.24	7.24	6.92
Caprellidea	0.28	0.33	0.24	0.20
Reptantia	1.36	2.01	2.54	3.44
Bryozoa	0.16	0.19	0.12	0.22
Diet quality	30.19	30.05	30.84	29.80
Pop. size	1.91	1.91	1.71	1.84
Catch	-	-	0.21	-

Table 39. Diet volume of prey in percent by taxonomic group for the diet of black perch, Embiotoca jackonsi, from the stochastic model for the four harvesting regimes.

	Harvesting Regime			
	No Harves- -ting	Single Spec.	Status Quo	Multi Spec.
Algae	1.12	0.78	0.75	0.96
Foraminifera	0.30	0.29	0.28	0.30
Porifera	0.	0.01	0.	0.01
Hydrozoa	4.83	5.16	4.25	4.67
Polychaeta	4.74	5.20	5.28	5.62
Polyplocophora	0.	0.	0.03	0.05
Gastropoda	9.73	9.98	9.50	9.06
Bivalvia	1.45	1.34	1.17	1.31
Ostracoda	0.14	0.13	0.13	0.13
Harpacticoida	0.01	0.01	0.01	0.01
Cyclopoida	0.09	0.08	0.07	0.07
Mysidacea	0.45	0.55	0.60	0.56
Cumacea	1.17	1.31	1.21	1.21
Tanaidacea	5.34	5.40	5.21	5.24
Isopoda	4.52	4.52	4.43	4.40
Gammaridea	47.81	48.12	47.44	47.00
Caprellidea	7.49	7.75	7.84	7.78
Reptantia	1.13	0.50	0.92	1.02
Natantia	0.50	0.66	0.82	0.82
Bryozoa	0.04	0.02	0.02	0.05
Ophiuroidea	4.78	4.04	4.52	4.73
Echinoidea	0.44	0.44	1.11	0.51
Ascidiacea	3.92	3.71	3.79	3.47
Entoprocta	-	-	-	-
Diet quality	7.02	7.07	7.14	6.96
Pop. size	2.09	2.10	1.86	2.06
Catch	-	-	0.24	-

Table 40. Diet volume of prey in percent by taxonomic group for the diet of sheephead (lg., >150 mm), Semicossyphus pulcher, from the stochastic model for the four harvesting regimes.

	Harvesting Regime			
	No Harves- -ting	Single Spec.	Status Quo	Multi Spec.
Fish	5.25	6.75	8.36	7.41
Algae	2.77	2.79	2.73	2.69
Foraminifera	0.08	0.09	0.08	0.08
Porifera	0.47	0.47	0.47	0.47
Hydrozoa	0.29	0.31	0.28	0.32
Anthozoa	3.78	3.82	4.16	3.72
Nemertea	0.	0.	0.	0.
Polychaeta	17.97	17.50	17.12	17.07
Polyplacophora	0.51	0.62	0.57	0.55
Gastropoda	29.88	28.65	28.57	28.61
Bivalvia	12.40	12.33	11.92	11.93
Pycnogonida	0.48	0.46	0.48	0.51
Ostracoda	0.	0.	0.	0.
Cirripedia	9.45	9.36	8.94	8.93
Cumacea	0.05	0.05	0.04	0.06
Tanaidacea	0.04	0.04	0.04	0.04
Isopoda	2.44	2.38	2.21	2.18
Gammaridea	6.04	5.96	5.74	5.66
Caprellidea	3.34	3.40	3.32	3.32
Reptantia	1.52	1.57	1.58	2.15
Natantia	0.61	0.76	0.52	1.60
Bryozoa	0.06	0.07	0.06	0.08
Ophiuroidea	1.46	1.44	1.67	1.57
Echinoidea	0.36	0.48	0.42	0.29
Holothuroidea	0.	0.	0.	0.
Ascidiacea	0.74	0.76	0.73	0.77
Diet quality	8.11	7.99	8.27	7.91
Pop. size	6.20	6.14	4.97	6.10
Catch	-	-	0.81	-

and in some cases, population increases. The increase in average length of time required to reach equilibrium under harvesting (15 years for no harvesting, 17 years for single species and status quo) resulted from an increase in the length of time kelp bass population and catch needed to stabilize. In both single species and status quo harvesting, kelp bass was the last fish species to stabilize and the increase in time to equilibrium represents a decrease in stability that results from harvesting. The results of the status quo harvesting are virtually identical to those of the single species harvesting. In terms of harvesting goals (increasing the catch of kelp bass) and community interactions, there is no difference between the two harvesting regimes.

The stochastic model displays the same patterns as those generated by the static model except that the impact of harvesting was much less dramatic. Since population size was fixed in the static model, catch cannot be compared between the two models, but diet quality of kelp bass increased between single species and multispecies harvesting 35.1% in the static model versus 11.1% in the stochastic model, a three fold difference (Tables 22 and 37). The fifteen species can still be divided into three groups; dietary winners, dietary losers and dietary neutrals; but the changes in diet and population sizes are much smaller, in many cases nonsignificant. The principal source of change is again from the release of reptantian and natantian decapod prey. These prey are highly selected by kelp bass whose increased catch is the management goal in the stochastic model.

The dietary winners: kelp bass (Table 37), small rock wrasse (Table 41), island kelpfish (Table 42) and blackeye goby (Table 43), all had increases in population sizes and catches from single species to multispecies harvesting. However diet quality levels of all of these fishes were lower than they were in the static model. Diet quality of kelp bass for the stochastic model was 76% of diet quality for the static model, for small rock wrasse 68%, for island kelpfish 38% and for blackeye goby 89%. The overall result of adding long term population dynamics to the model structure was a reduction of the size of dietary response to harvesting by dietary winners. As in the static model, these species represent the fish predators with above average selectivity for the two decapod groups. The increased diet share of these two decapod groups by fishes under multispecies harvesting increased their overall diet quality, their population sizes and catches.

The dietary losers were painted greenling (Table 44), opaleye (Table 38), black perch (Table 39), Garibaldi (Table 45), large rock wrasse (Table 46), small and large sheephead (Tables 47 and 40) and spotted kelpfish (Table 48). All had decreased population sizes; however none of the decreases were larger than 3% and small sheephead only decreased 0.6%. As in the static model, the response of the dietary losers was of much smaller magnitude than that of the dietary winners. Two factors, 1) overall reduction of impact of harvesting in the stochastic model as compared to the static model and 2) much smaller magnitude of response of the dietary losers as compared to the dietary winners, combined to account for the very small amount of change

Table 41. Diet volume of prey in percent by taxonomic group for the diet of rock wrasse, (sm., <150 mm), Halichoeres semicinctus, from the stochastic model for the four harvesting regimes.

	Harvesting Regime			
	No Harves- -ting	Single Spec.	Status Quo	Multi Spec.
Fish eggs	0.	0.	0.01	0.
Algae	0.59	0.36	0.63	0.45
Hydrozoa	1.13	0.81	0.74	0.81
Polychaeta	7.83	8.27	8.41	8.03
Gastropoda	10.60	11.58	10.79	10.16
Bivalvia	7.76	7.48	7.42	7.18
Pycnogonida	0.04	0.06	0.05	0.11
Ostracoda	2.18	2.09	2.10	1.96
Cirripedia	0.05	0.08	0.05	0.04
Cumacea	0.31	0.30	0.34	0.30
Tanaidacea	0.46	0.44	0.43	0.40
Isopoda	7.11	7.15	7.10	6.38
Gammaridea	34.79	33.26	33.71	30.53
Caprellidea	10.61	10.39	10.85	9.40
Reptantia	3.23	4.17	2.84	6.03
Natantia	1.74	2.20	3.07	6.41
Bryozoa	0.78	0.75	0.54	0.89
Ophiuroidea	7.33	7.19	7.79	7.64
Ascidacea	3.45	3.44	3.12	3.28
Diet quality	6.09	6.11	6.16	6.52
Pop. size	1.53	1.54	1.53	1.59
Catch	-	-	-	-

Table 42. Diet volume of prey in percent by taxonomic group for the diet of island kelpfish, Alloclinus holderi, from the stochastic model for the four harvesting regimes.

	Harvesting Regime			
	No Harves- -ting	Single Spec.	Status Quo	Multi Spec.
Fish eggs	0.18	0.17	0.17	0.16
Polychaeta	2.22	2.26	2.48	2.20
Gastropoda	1.30	1.31	1.35	1.10
Veleger	0.10	0.08	0.08	0.04
Bivalvia	0.42	0.41	0.44	0.37
Ostracoda	0.09	0.09	0.09	0.08
Harpacticoida	0.11	0.11	0.11	0.10
Mysidacea	0.46	0.63	0.56	0.53
Cumacea	2.70	2.69	2.65	2.34
Isopoda	15.07	15.35	14.89	13.41
Gammaridea	44.91	45.13	44.80	40.62
Caprellidea	24.06	24.67	24.65	23.26
Reptantia	5.81	4.90	4.90	6.99
Natantia	2.57	2.17	2.84	8.83
Diet quality	10.41	10.09	10.22	12.04
Pop. size	4.67	4.58	4.61	2.76
Catch	-	-	-	2.10

Table 43. Diet volume of prey in percent by taxonomic group for the diet of blackeye goby, *Coryphopterus nicholsii*, from the stochastic model for the four harvesting regimes.

	Harvesting Regime			
	No Harves -ting	Single Spec.	Status Quo	Multi Spec.
Fish	0.14	0.	0.24	0.15
Fish eggs	0.	0.	0.	0.
Algae	5.34	4.97	4.74	4.87
Foraminifera	0.50	0.49	0.48	0.47
Porifera	0.28	0.26	0.23	0.27
Nemertea	0.05	0.05	0.05	0.05
Polychaeta	20.06	20.71	20.18	19.29
Polyplacophora	0.36	0.12	0.28	0.22
Gastropoda	14.68	15.45	15.48	14.40
Bivalvia	2.32	2.20	2.37	2.24
Pycnogonida	1.76	1.55	1.81	1.45
Ostracoda	0.26	0.26	0.26	0.25
Calanoida	9.78	9.78	9.79	9.24
Harpacticoida	0.14	0.14	0.15	0.14
Cyclopoida	0.43	0.45	0.42	0.41
Cumacea	5.18	5.20	5.25	4.93
Tanaidacea	4.26	4.16	4.16	3.93
Isopoda	7.15	6.93	7.32	6.70
Gammaridea	15.79	15.83	15.86	15.10
Caprellidea	2.95	3.00	2.95	2.79
Reptantia	0.94	1.45	0.61	1.50
Natantia	1.79	1.70	2.13	6.34
Bryozoa	0.02	0.02	0.01	0.02
Ophiuroidea	5.16	4.82	4.83	4.57
Echinoidea	0.63	0.48	0.40	0.64
Diet quality	5.43	5.45	5.43	5.67
Pop. size	6.54	6.56	6.55	5.04
Catch	-	-	-	2.62

Table 44. Diet volume of prey in percent by taxonomic group for the diet of painted greenling, Oxylebius pictus, from the stochastic model for the four harvesting regimes.

	Harvesting Regime			
	No Harves- -ting	Single Spec.	Status Quo	Multi Spec.
Fish	3.21	3.29	3.75	3.55
Fish eggs	0.09	0.	0.08	0.10
Fish larva	1.21	1.56	1.22	1.28
Algae	0.11	0.08	0.05	0.07
Hydrozoa	4.36	4.25	4.39	4.43
Polychaeta	5.64	5.25	5.52	5.28
Gastropoda	1.02	0.94	1.14	0.96
Bivalvia	0.33	0.37	0.36	0.35
Pycnogonida	0.32	0.24	0.36	0.38
Ostracoda	0.03	0.03	0.03	0.03
Cirripedia	3.67	3.68	3.62	3.65
Tanaidacea	0.10	0.10	0.10	0.10
Isopoda	14.95	14.38	14.38	14.41
Gammaridea	39.49	38.63	38.63	38.02
Caprellidea	23.52	23.88	23.88	23.65
Reptantia	1.54	1.71	1.71	2.30
Natantia	0.40	0.80	0.80	1.45
Bryozoa	0.	0.	0.	0.
Diet quality	12.71	12.76	12.65	12.47
Pop. size	1.54	1.54	1.54	1.50
Catch	-	-	-	-

Table 45. Diet volume of prey in percent by taxonomic group for the diet of Garibaldi, Hypsypops rubicundus, from the stochastic model for the four harvesting regimes.

	Harvesting Regime			
	No Harves- -ting	Single Spec.	Status Quo	Multi Spec.
Fish	2.01	2.69	3.30	2.95
Algae	52.56	53.69	52.74	50.91
Foraminifera	0.48	0.48	0.47	0.48
Porifera	0.46	0.42	0.37	0.43
Hydrozoa	4.46	4.24	4.27	4.01
Anthozoa	2.37	2.14	2.10	2.21
Polychaeta	2.93	2.29	2.37	2.62
Gastropoda	3.55	3.26	3.65	3.48
Bivalvia	0.95	0.77	0.88	0.82
Cephalopoda	0.	0.01	0.	0.
Ostracoda	0.06	0.07	0.06	0.06
Harpacticoida	0.04	0.04	0.04	0.04
Cirripedia	5.00	4.91	5.02	4.61
Tanaidacea	0.01	0.01	0.01	0.01
Isopoda	0.05	0.05	0.06	0.04
Gammaridea	13.87	13.77	13.77	13.22
Caprellidea	0.11	0.11	0.10	0.10
Reptantia	2.91	3.01	2.99	5.40
Bryozoa	0.84	0.74	0.57	1.01
Asteroidea	2.13	1.96	1.96	1.91
Ophiuroidea	0.44	0.59	0.39	0.70
Ascidiacea	4.78	4.81	4.87	4.99
Diet quality	14.95	15.15	14.92	14.60
Pop. size	3.92	3.98	3.92	3.82
Catch	-	-	-	-

Table 46. Diet volume of prey in percent by taxonomic group for the diet of rock wrasse (lg., >150 mm), Halichoeres semicinctus, from the stochastic model for the four harvesting regimes.

	Harvesting Regime			
	No Harves- -ting	Single Spec.	Status Quo	Multi Spec.
Fish eggs	0.17	0.16	0.19	0.13
Algae	8.95	8.31	8.56	8.74
Foraminifera	0.07	0.07	0.07	0.07
Porifera	0.90	0.95	0.91	0.81
Hydrozoa	0.13	0.12	0.14	0.16
Nemertea	0.29	0.27	0.25	0.29
Polychaeta	6.40	6.36	6.49	6.26
Polyplacophora	0.30	0.51	0.59	0.66
Gastropoda	14.60	14.21	13.99	13.66
Bivalvia	6.42	6.28	6.47	5.92
Pycnogonida	0.57	0.79	0.55	0.55
Ostracoda	0.02	0.02	0.02	0.02
Harpacticoida	0.91	0.91	0.89	0.86
Cirripedia	0.55	0.59	0.54	0.54
Mysidacea	0.19	0.24	0.24	0.21
Cumacea	0.28	0.30	0.28	0.27
Tanaidacea	2.15	2.20	2.13	2.04
Isopoda	5.74	5.92	5.79	5.61
Gammaridea	19.29	19.55	18.98	18.52
Caprellidea	21.37	22.17	21.47	21.01
Reptantia	0.97	0.82	1.50	2.08
Natantia	0.54	0.54	0.81	2.14
Bryozoa	0.47	0.40	0.35	0.59
Asteroidea	0.20	0.16	0.18	0.19
Ophiuroidea	5.63	5.05	5.44	5.18
Echinoidea	0.56	0.70	0.74	1.08
Ascidacea	2.34	2.41	2.46	2.41
Diet quality	5.37	5.39	5.38	5.30
Pop. size	5.58	5.58	5.55	5.56
Catch	-	-	0.02	-

Table 47. Diet volume of prey in percent by taxonomic group for the diet of sheephead (sm., <150 mm), Semicossyphus pulcher, from the stochastic model for the four harvesting regimes.

	Harvesting Regime			
	No Harves- -ting	Single Spec.	Status Quo	Multi Spec.
Fish eggs	0.12	0.14	0.13	0.19
Nemertea	0.69	0.76	0.72	0.71
Polychaeta	20.82	21.25	21.69	20.30
Polyplocophora	0.	0.03	0.04	0.04
Gastropoda	12.24	13.01	11.81	11.79
Bivalvia	9.14	9.04	8.76	8.24
Ostracoda	0.95	0.96	0.94	0.91
Cyclopoida	3.54	3.42	3.40	3.34
Caligoida	0.	0.	0.	0.
Tanaidacea	2.31	2.38	2.33	2.25
Isopoda	6.82	7.08	6.95	6.74
Gammaridea	35.39	33.29	35.13	33.64
Caprellidea	0.86	0.85	0.88	0.80
Reptantia	2.36	1.59	1.59	3.30
Natantia	0.91	0.84	0.76	0.83
Ophiuroidea	2.50	2.69	1.83	2.25
Echinoidea	1.37	0.68	0.68	1.68
Diet quality	6.48	6.34	6.56	6.34
Pop. size	2.08	2.05	2.09	2.06
Catch	-	-	-	-

Table 48. Diet volume of prey in percent by taxonomic group for the diet of spotted kelpfish, Gibbonsia elegans, from the stochastic model for the four harvesting regimes.

	Harvesting Regime			
	No Harves- -ting	Single Spec.	Status Quo	Multi Spec.
Fish	0.	0.09	0.15	0.10
Fish eggs	0.01	0.	0.	0.
Algae	1.85	1.98	1.89	1.81
Foraminifera	0.72	0.74	0.73	0.70
Polychaeta	3.16	3.42	3.58	3.26
Gastropoda	2.85	2.85	2.77	2.60
Cladocera	0.	0.	0.	0.
Ostracoda	0.02	0.02	0.02	0.02
Calanoida	0.11	0.10	0.10	0.10
Cirripedia	0.07	0.07	0.08	0.08
Isopoda	28.45	28.35	28.56	27.16
Gammaridea	52.16	52.23	52.09	50.70
Caprellidea	8.17	8.15	8.21	8.21
Reptantia	1.56	1.51	1.33	2.48
Natantia	0.86	0.49	0.48	2.79
Diet quality	14.59	14.55	14.56	14.31
Pop. size	0.17	0.16	0.16	0.14
Catch	-	-	-	-

in population sizes in this group of fishes. These were the fishes that had a lower selectivity for the two decapod groups and so an increasing dietary share of these prey groups resulted in lower dietary quality and lower population sizes.

The dietary neutral (or trophically isolated) species: pile perch (Table 49), small and large seniorita (Tables 50 and 51) did not change over any of the harvesting regimes. These species either had no or very low increases in the two decapod prey categories reflecting either a zero or very low selectivity for these two decapod prey. They are, in the trophic sense, disconnected from the rest of the species in the model.

In summary, the general pattern of fish species response to multispecies harvesting in terms of dietary winners, dietary losers and dietary neutrals was similar in the stochastic model to the static model, but the magnitude of that response was much smaller. This reduction in response is attributed to the compensatory effects of the addition of long term population dynamics. The mechanism that controls the changes occurring with multispecies harvesting was the two decapods prey groups. These were large volume prey which were highly selected by kelp bass and so that release of even very small numbers of these prey can have large impact on their diet.

In both the static and the stochastic models, the same three of the fifteen fish species were used in the multispecies harvesting regime: large rock wrasse, island kelpfish and blackeye goby. The question arises how much more effective, in terms of increasing the catch of kelp bass, is the multispecies

Table 49. Diet volume of prey in percent by taxonomic group for the diet of pile perch, Damalichthys vacca, from the stochastic model for the four harvesting regimes.

	Harvesting Regime			
	No Harves- -ting	Single Spec.	Status Quo	Multi Spec.
Polychaeta	2.20	2.35	2.48	2.78
Gastropoda	51.41	50.41	51.00	51.21
Bivalvia	41.89	42.23	42.42	42.89
Isopoda	0.10	0.10	0.12	0.11
Gammaridea	0.51	0.51	0.57	0.48
Ophiuroidea	2.49	3.25	2.49	2.07
Echinoidea	1.20	1.14	0.94	0.46
Diet quality	34.16	34.10	34.24	34.45
Pop. size	1.27	1.27	1.23	1.28
Catch	-	-	-	-

Table 50. Diet volume of prey in percent by taxonomic group for the diet of *senorita* (sm., <150 mm), *Oxyjulis californica*, from the stochastic model for the four harvesting regimes.

	Harvesting Regime			
	No Harves- -ting	Single Spec.	Status Quo	Multi Spec.
Fish eggs	0.	0.01	0.01	0.01
Algae	13.33	12.37	13.65	13.50
Porifera	0.01	0.	0.01	0.01
Hydrozoa	4.17	4.31	4.17	3.95
Polychaeta	16.41	17.44	16.55	17.55
Gastropoda	1.52	1.31	1.47	1.37
Veleger	0.37	0.53	0.39	0.57
Bivalvia	1.44	1.19	1.22	1.32
Pycnogonida	0.	0.02	0.04	0.07
Cladocera	0.	0.	0.	0.
Ostracoda	0.	0.	0.	0.
Calanoida	6.32	6.15	6.43	6.25
Harpacticoida	0.05	0.04	0.04	0.04
Cyclopoida	0.12	0.13	0.12	0.11
Caligoida	0.10	0.09	0.08	0.06
Cirripedia	1.09	1.32	1.12	1.25
Tanaidacea	0.05	0.05	0.04	0.05
Isopoda	18.91	18.39	18.68	17.73
Gammaridea	15.64	15.52	15.63	14.68
Caprellidea	18.85	19.09	18.86	18.25
Euphausiacea	0.07	0.	0.07	0.08
Natantia	0.	0.18	0.12	1.04
Insecta	0.	0.	0.	0.
Bryozoa	1.56	1.32	1.27	2.10
Ophiuroidea	0.	0.05	0.04	0.
Echinoidea	0.	0.	0.	0.
Diet quality	8.63	8.64	8.59	8.62
Pop. size	14.16	14.15	14.11	14.11
Catch	-	-	-	-

Table 51. Diet volume of prey in percent by taxonomic group for the diet of seniorita (lg., >150 mm), Oxyjulis californica, from the stochastic model for the four harvesting regimes.

	Harvesting Regime			
	No Harves- -ting	Single Spec.	Status Quo	Multi Spec.
Fish eggs	0.01	0.	0.01	0.01
Algae	26.18	26.46	26.36	26.46
Polychaeta	19.36	19.32	20.50	18.43
Polyplacophora	0.45	0.15	0.40	0.80
Gastropoda	13.07	12.88	12.12	12.89
Bivalvia	0.47	0.50	0.41	0.45
Cladocera	0.01	0.01	0.01	0.01
Ostracoda	0.	0.	0.	0.
Calanoida	14.54	15.05	14.77	14.51
Harpacticoida	0.10	0.10	0.10	0.09
Cyclopoida	0.36	0.43	0.42	0.41
Caligoida	0.04	0.03	0.03	0.02
Mysidacea	0.02	0.01	0.01	0.01
Isopoda	2.97	2.78	2.70	2.68
Gammaridea	5.91	6.10	5.95	5.73
Caprellidea	7.32	7.48	7.33	7.31
Natantia	0.	0.	0.	0.13
Bryozoa	1.69	1.72	1.35	2.16
Ophiuroidea	6.81	6.42	6.68	7.09
Echinoidea	0.12	0.08	0.18	0.12
Ascidiacea	0.57	0.50	0.64	0.70
Diet quality	10.57	10.64	10.63	10.63
Pop. size	8.97	9.01	8.90	9.00
Catch	-	-	0.09	-

harvesting regime than alternative ones. Is one multispecies harvesting regime superior to other possible multispecies harvesting regimes and if so, how much more superior? In order to test these questions, model runs were made with three different alternative multispecies harvesting regimes each with a fishing mortality of 0.38 for kelp bass and a fishing mortality of 0.76 for one of the three species listed above. For reference, catch from single species harvesting (kelp bass, $F=0.38$) catch was 0.147 individuals/year and from multispecies harvesting (kelp bass $F=0.38$, island kelpfish and blackeye goby, $F=0.76$) was 0.168 individuals/year. The first alternative harvesting regime, harvesting island kelpfish along with kelp bass, resulted in an increase in the catch of kelp bass to 0.160 individuals/year, an 8.8% increase. The second alternative harvesting regime, harvesting of blackeye goby along with kelp bass, increased kelp bass catch to 0.150 (a 2.0% increase) and the final alternative harvesting regime, harvesting of large rock wrasse along with kelp bass, increased catch to 0.152 (a 3.4% increase). The first step of the multispecies harvesting regime (island kelpfish and kelp bass) was superior in meeting management goals to the other alternate harvesting regimes by a large margin. No alternate harvesting regime was even one half as effective as the first step of the multispecies harvesting regime. It is interesting to note that the order that fishes were added to the multispecies harvesting plan is not the same as the relative order of effectiveness (the amount of increase in kelp base catch) found here when these species harvested individually along with kelp bass.

The variation in response of kelp bass populations within each of the four harvesting regimes: no harvesting, single species, status quo and multispecies harvesting, was very similar. Typically the variation in population size climbed quickly to a maximum (usually to a coefficient of variation of around 30%) in the first few years and then it would gradually reduce to a very small value. An example of this were the runs from the no harvesting regime (Figure 2). Only five of thirteen runs are shown here. These five runs were the ones with the most extreme differences. The runs all started off at the same initial value and by year two, the largest difference between runs had occurred. From this point, populations from all runs gradually approach a common equilibrium.

The twelve model runs from the single species harvesting regime were divided up into two nonoverlapping groups; five runs that reached equilibrium in 14 or 15 years and seven runs that reached equilibrium in 19 or 20 years (Figure 3). Even though the mean equilibrium populations of the groups were only different by 0.02 individuals (14 or 15 years 0.49 versus 19 or 20 years 0.47), the means were significantly different at 10% level ($t = 1.81$, d.f. = 10). They also differed in that the group that reach equilibrium in 14 or 15 years gradually declined to equilibrium while the group that reach equilibrium in 19 or 20 years dropped below the equilibrium and then gradually increased toward it.

The average response of kelp bass population under all harvesting regimes was roughly a decaying curve to equilibrium

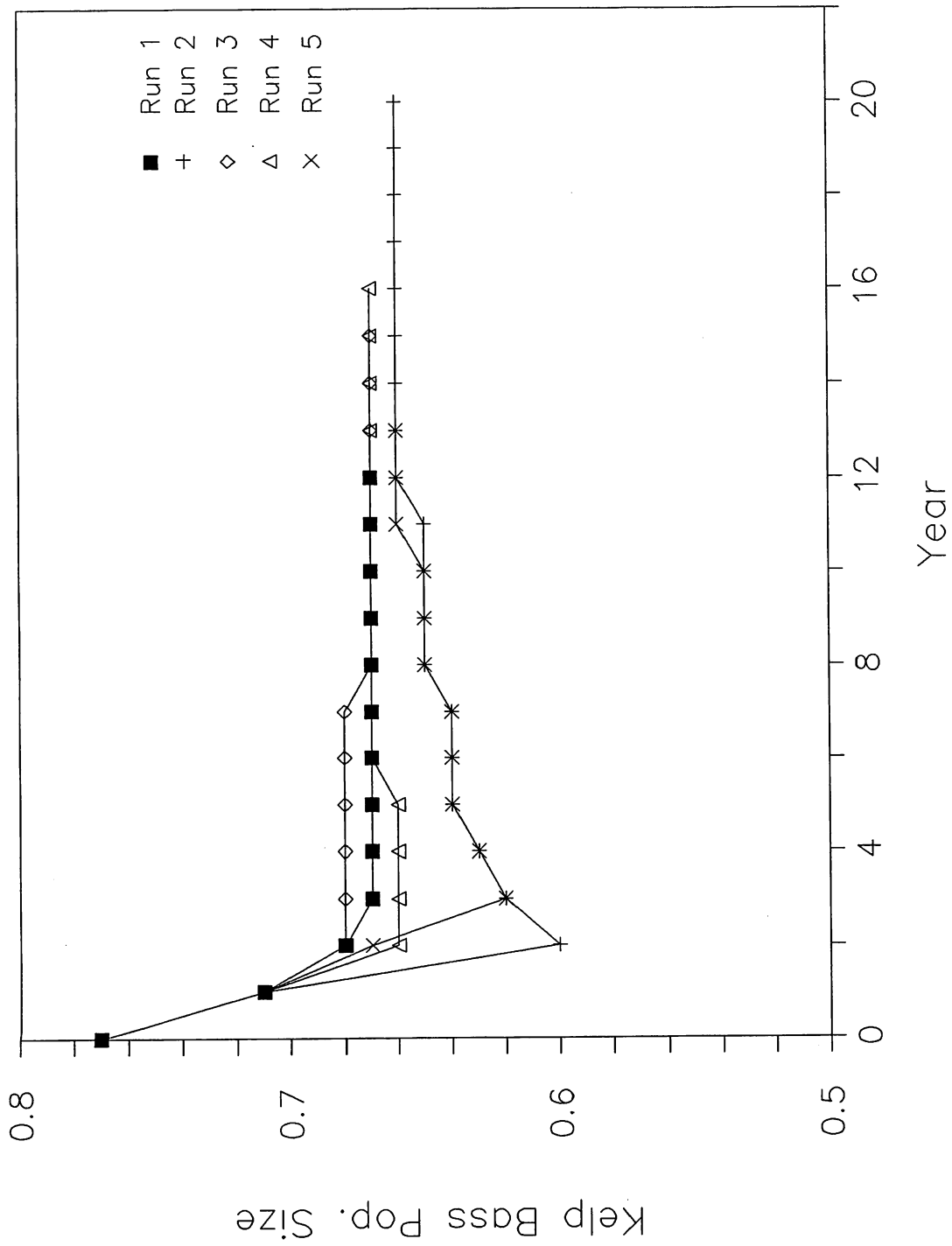


Figure 2. Kelp bass population size during five model runs from the no harvesting regime of the stochastic model.

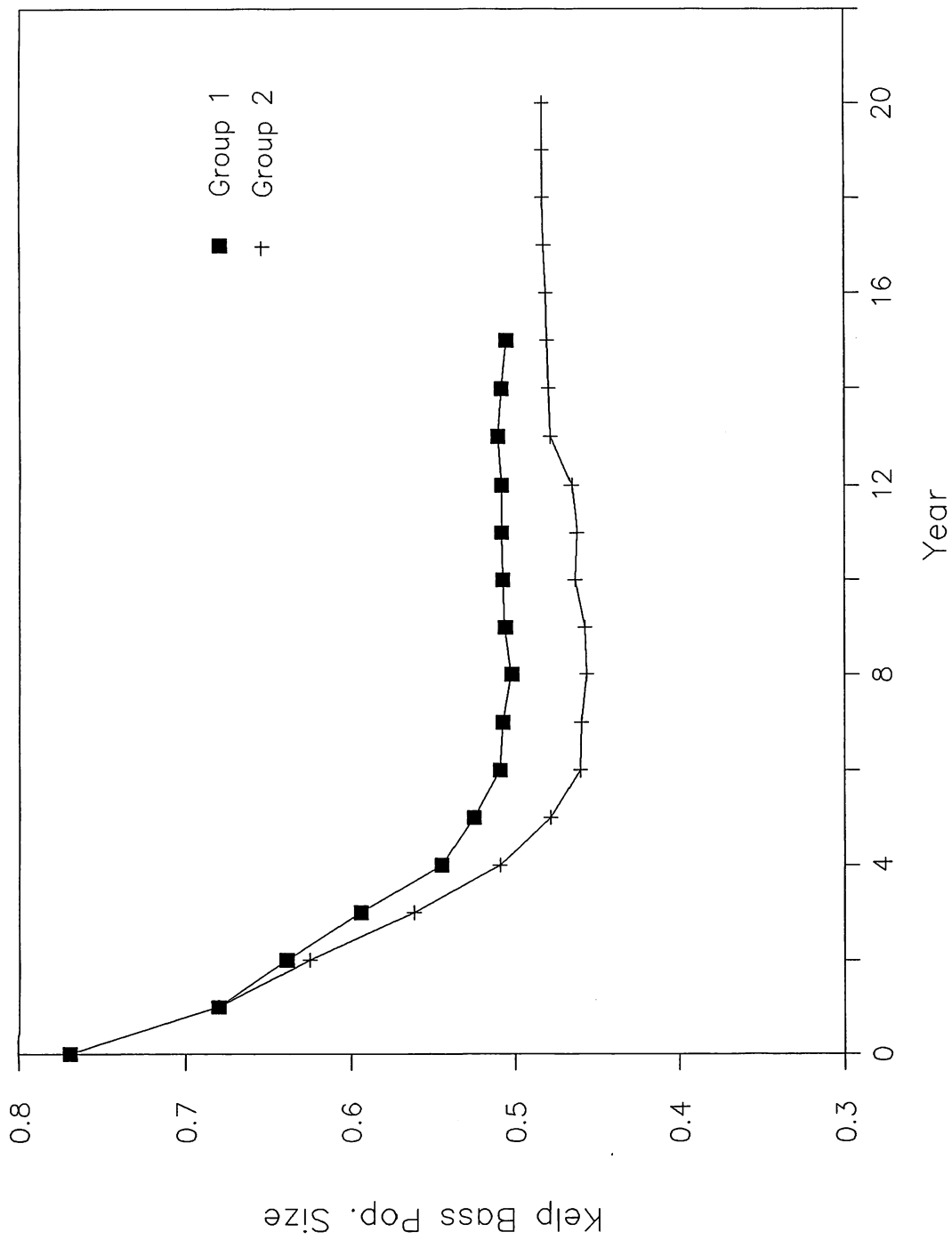


Figure 3. For single species harvesting of the stochastic model, average keep bass population sizes divided into two groups. Group 1 was the average of five runs which reached equilibrium in 14 or 15 years. Group 2 was the average of seven runs that reached equilibrium in 19 or 20 years.

with time (Figure 4). The large drop in population size between the 15th and 16th year for the multispecies harvesting was artificial. Only one model run went out to 16 years and all population sizes in that run were all low. So in year fifteen, five runs were averaged, but in year sixteen, the average population size was only one point and hence the drop in average population size. There are two important points about the multispecies harvesting regime. The first is that the model came to equilibrium much faster than for the harvesting regimes. The second is that not only is the endpoint of population size higher than single species or status quo harvesting, but earlier in the model runs, multispecies harvesting population sizes are actually relatively higher than single species or status quo harvesting. Finally, population sizes of single species and status quo model conditions were virtually identical.

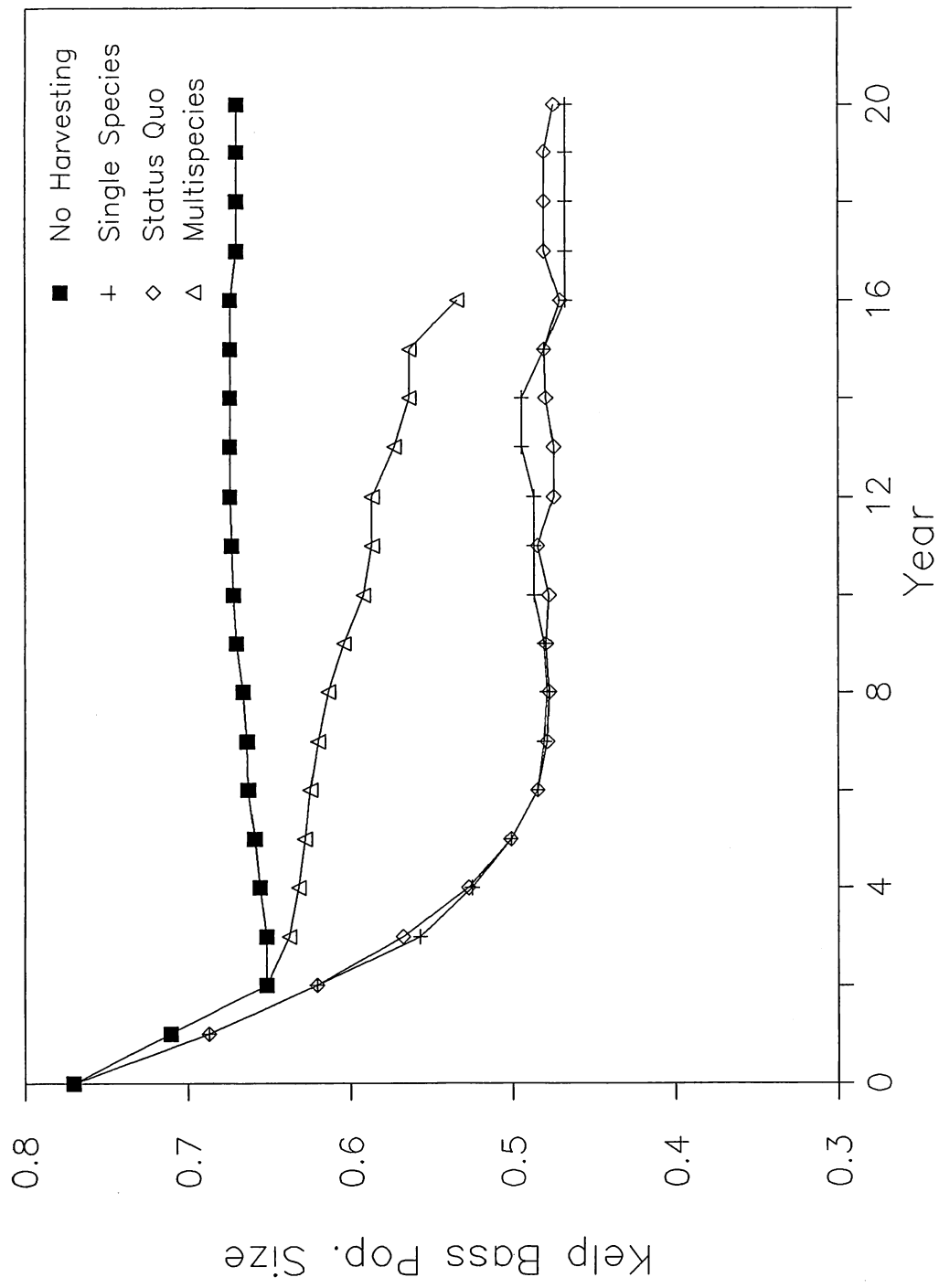


Figure 4. Average kelp bass population sizes from the stochastic model under the four harvesting regimes (no harvesting, single species, status quo and multispecies).

Deterministic Model

The results of the first three harvesting regimes with deterministic feeding: no harvesting, single species and status quo harvesting, were dramatically different from those of the stochastic model. The runs came to equilibrium in a much shorter period of time (11 versus 16.3 years). The diets of fishes in these runs followed the distribution of prey in the environment more closely than in the stochastic model (Tables 52 to 66). As an example, gammarid and caprellid amphipods were the two most abundant prey groups, making up almost 40% of the total prey. In the thirty-nine instances in which fishes were feeding on these two prey groups under the no harvesting regime, thirty-eight had exhibited increases of these two prey in their diet when comparing the stochastic and deterministic models; sometimes the increase doubled. For most fishes, this resulted in an increase in diet quality and population, but for fishes with more specialized diets (high selectivity for one or two low abundance prey), it meant a decrease. All of the fishes in which population size decreased when comparing the stochastic and deterministic models had specialized diets. Opaleye (Table 52) and Garibaldi (Table 53) both feed on algae and encrusting animals. Pile perch (Table 54) and to a much lesser degree large sheephead (Table 55) are mollusk feeders and both had substantial reductions in the amount of gastropods in their diet. Island kelpfish (Table 56), although not strictly a specialist, had very high selectivity for the two decapod groups: reptantia and natantia.

In the deterministic model compared to the stochastic

Table 52. Diet volume of prey in percent by taxonomic group for the diet of opaleye, Girella nigricans, from the deterministic model for the four harvesting regimes.

	Harvesting Regime			
	No Harves- -ting	Single Spec.	Status Quo	Multi Spec.
Algae	23.35	23.29	24.32	18.92
Hydrozoa	2.79	2.86	3.02	2.21
Gastropoda	.08	.09	.23	.06
Ostracoda	7.25	7.04	6.84	4.96
Harpacticoida	25.14	26.08	25.44	50.74
Cyclopoida	.08	.08	.08	.06
Isopoda	11.41	11.20	10.99	8.18
Gammaridea	24.86	24.39	24.00	10.91
Caprellidea	.67	.72	.73	.92
Reptantia	.29	.32	.59	.25
Bryozoa	4.06	3.93	3.76	2.80
Diet quality	14.07	14.18	14.52	15.36
Pop. size	1.30	1.30	1.04	1.33
Catch	-	-	0.17	-

Table 53. Diet volume of prey in percent by taxonomic group for the diet of Garibaldi, Hypsypops rubicundus, from the deterministic model for the four harvesting regimes.

	Harvesting Regime			
	No Harves- -ting	Single Spec.	Status Quo	Multi Spec.
Fish	0.84	0.82	0.80	0.91
Algae	14.95	15.19	15.82	19.42
Foraminifera	6.94	6.90	6.86	8.27
Porifera	0.49	0.48	0.48	0.56
Hydrozoa	1.44	1.50	1.58	1.83
Anthozoa	0.91	0.94	1.15	1.11
Polychaeta	0.17	0.19	0.34	0.31
Gastropoda	0.19	0.20	0.53	0.23
Bivalvia	0.06	0.06	0.12	0.06
Cephalopoda	0.00	0.00	0.00	0.00
Ostracoda	2.00	1.98	1.91	2.20
Harpacticoida	1.23	1.30	1.26	3.97
Cirripedia	5.90	5.84	5.78	6.52
Tanaidacea	0.13	0.13	0.13	0.17
Isopoda	0.09	0.09	0.08	0.10
Gammaridea	43.17	43.13	42.27	30.29
Caprellidea	0.25	0.27	0.27	0.54
Reptantia	0.50	0.55	1.01	0.67
Bryozoa	16.08	15.84	15.09	17.74
Asteroidea	0.42	0.41	0.45	0.48
Ophiuroidea	0.03	0.03	0.04	0.04
Ascidacea	4.22	4.15	4.01	4.59
Diet quality	7.79	7.83	7.95	9.03
Pop. size	2.77	2.77	2.79	2.97
Catch	-	-	-	-

Table 54. Diet volume of prey in percent by taxonomic group for the diet of pile perch, Damalichthys vacca, from the deterministic model for the four harvesting regimes.

	Harvesting Regime			
	No Harves- -ting	Single Spec.	Status Quo	Multi Spec.
Polychaeta	2.78	3.15	2.06	7.18
Gastropoda	28.26	30.33	55.88	34.23
Bivalvia	11.63	11.77	26.10	10.79
Isopoda	4.45	4.22	1.13	5.42
Gammaridea	50.24	47.66	12.83	37.47
Ophiuroidea	2.43	2.64	1.56	4.57
Echinoidea	0.22	0.23	0.44	0.35
Diet quality	12.25	12.73	25.62	13.09
Pop. size	0.91	0.91	1.12	0.91
Catch	-	-	0.17	-

Table 55. Diet volume of prey in percent by taxonomic group for the diet of sheephead (lg., >150 mm), Semicossyphus pulcher, from the deterministic model for the four harvesting regimes.

	Harvesting Regime			
	No Harves- -ting	Single Spec.	Status Quo	Multi Spec.
Fish	6.33	6.13	5.45	5.87
Algae	1.37	1.36	1.31	1.51
Foraminifera	1.97	1.93	1.76	2.00
Porifera	0.93	0.90	0.82	0.90
Hydrozoa	0.16	0.16	0.16	0.17
Anthozoa	3.31	3.36	3.78	3.43
Nemertea	0.02	0.02	0.02	0.02
Polychaeta	2.00	2.17	3.66	3.15
Polyplacophora	0.12	0.11	0.10	0.11
Gastropoda	2.63	2.73	7.07	2.77
Bivalvia	1.22	1.22	2.64	1.10
Pycnogonida	0.25	0.24	0.21	0.23
Ostracoda	0.08	0.08	0.07	0.08
Cirripedia	18.94	18.38	16.72	17.75
Cumacea	0.13	0.13	0.11	0.12
Tanaidacea	1.04	1.04	.93	1.20
Isopoda	5.56	5.46	4.90	5.44
Gammaridea	32.27	31.68	28.53	19.29
Caprellidea	14.83	15.96	14.76	27.79
Reptantia	0.71	0.78	1.38	0.84
Natantia	0.85	1.02	0.95	1.19
Bryozoa	4.08	3.95	3.46	3.86
Ophiuroidea	0.13	0.14	0.21	0.18
Echinoidea	0.03	0.03	0.07	0.04
Holothuroidea	0.00	0.00	0.00	0.00
Asciacea	1.05	1.02	0.90	0.97
Diet quality	3.38	3.40	4.08	3.60
Pop. size	4.28	4.28	3.58	4.28
Catch	-	-	0.72	-

Table 56. Diet volume of prey in percent by taxonomic group for the diet of island kelpfish, Alloclinus holderi, from the deterministic model for the four harvesting regimes.

	Harvesting Regime			
	No Harves- -ting	Single Spec.	Status Quo	Multi Spec.
Fish eggs	0.10	0.10	0.10	0.09
Polychaeta	0.06	0.07	0.12	0.09
Gastropoda	0.03	0.03	0.07	0.03
Veliger	0.01	0.01	0.01	0.01
Bivalvia	0.01	0.01	0.02	0.01
Ostracoda	1.00	0.96	0.93	0.90
Harpacticoida	1.15	1.18	1.15	3.08
Mysidacea	0.57	0.55	0.53	0.51
Cumacea	1.59	1.51	1.46	1.41
Isopoda	7.97	7.72	7.53	7.47
Gammaridea	56.48	54.72	53.53	32.38
Caprellidae	28.02	29.72	29.92	50.29
Reptantia	1.31	1.42	2.61	1.46
Natantia	1.69	2.00	2.03	2.26
Diet quality	9.52	9.75	10.12	11.25
Pop. size	4.41	4.47	4.57	4.86
Catch	-	-	-	-

model, the prey species in the different fishes' diet that were common were more common, while the rare prey species in that fishes diet were more rare. Therefore, there were greater differences among the three harvesting regimes (no harvesting, single species and status quo) than in the stochastic model. Painted greenling (Table 57), and island kelpfish (Table 56), both had higher populations in single species harvesting regime than in no harvesting regime largely attributable to increases in the availability of caprellid amphipods. Status quo harvesting had the dramatic effect on pile perch of increasing diet quality by one half and increasing population size by one third (Table 54). This occurred because of the release of mollusks from predation pressure due to the harvesting of large sheephead. So in the deterministic model, there was substantial difference in the results between the harvesting regimes: no harvesting, single species and status quo harvesting.

The stronger emphasis that the deterministic model places on prey abundance was apparent both in the diet of the fishes from the different harvesting regimes, and in the differences in the diet of fishes between the single species and multispecies harvesting regimes. First in the construction of the multispecies harvesting regime, the order that fishes were added was different than that from the stochastic model. In the actual deterministic multispecies harvesting regime, the increase in population size and catch of kelp bass was not due to increases in the diet of the large, highly selective, rare decapods as in the stochastic model, but due to increases of caprellid amphipods

Table 57. Diet volume of prey in percent by taxonomic group for the diet of painted greenling, Oxylebius pictus, from the deterministic model for the four harvesting regimes.

	Harvesting Regime			
	No Harves- -ting	Single Spec.	Status Quo	Multi Spec.
Fish	0.70	0.67	0.66	0.64
Fish eggs	0.06	0.06	0.06	0.06
Fish larva	0.03	0.03	0.03	0.02
Algae	0.01	0.01	0.01	0.01
Hydrozoa	0.61	0.62	0.66	0.64
Polychaeta	0.18	0.19	0.34	0.26
Gastropoda	0.03	0.03	0.08	0.03
Bivalvia	0.01	0.01	0.02	0.01
Pycnogonida	0.04	0.04	0.04	0.04
Ostracoda	0.40	0.39	0.38	0.37
Cirripedia	1.88	1.81	1.81	1.73
Tanaidacea	0.60	0.60	0.58	0.67
Isopoda	9.07	8.82	8.69	8.64
Gammaridea	56.05	54.54	53.83	32.68
Caprellidea	29.80	31.60	32.03	53.58
Reptantia	0.24	0.26	0.48	0.27
Natantia	0.24	0.28	0.29	0.32
Bryozoa	0.03	0.03	0.03	0.03
Diet quality	13.88	14.11	14.15	16.73
Pop. size	1.63	1.64	1.64	1.83
Catch	-	-	-	-

(increase in kelp bass diet volume of 4.28%) and harpactacoid copepods (increase of 16.01%). These prey are smaller, less highly selected, but much more abundant than the decapods. It was through redistribution of these different prey groups that multispecies harvesting operates given deterministic conditions.

Since these prey groups, caprellid amphipods and harpactocoid copepods, were widely taken (occurring in fourteen and nine of fifteen species, respectively) and were generally strongly selected prey among all the fishes, increases in their abundance during multispecies harvesting had a larger and more widespread impact on other fishes than did multispecies harvesting in the stochastic model. As a result, most fish species gained in both diet quality and population size from single species to multispecies harvesting (two fishes decreased in diet quality and only one actually decreased in population size). This pattern was further reinforced for many fishes by secondary harvesting effects through prey other than these two groups. For example, diet quality and population size of pile perch (Table 54) increased slightly due to increase in both ophiuroids and gastropods in the diet which, in turn, were released by harvesting of large rock wrasse. Because of this, the grouping of fishes into dietary winners, dietary losers and dietary neutrals was changed to two groups. Fish that exhibit substantial dietary quality and population size increase (greater than 5%) and those that did not.

The list of fishes which exhibited substantial increases in dietary quality and population size were: painted greenling (dietary quality 18%, population size 12%, Table 57), kelp bass

(24%, 19% Table 58), Garibaldi (15%, 9%, Table 53), large rock wrasse (23%, 12%, Table 59), small senorita (10%, 6%, Table 60) and island kelpfish (15%, 9%, Table 56). With the exception of Garibaldi, this is a list of the fishes that had strong selectivity for caprellid amphipods. The harvesting of large rock wrasse and blackeye goby, along with kelp bass, had increased the availability of this strongly selected, abundant prey and, in turn, it became more abundant in the diet of these fishes. The largest increase was exhibited by kelp bass. The harvesting also increased availability of another prey, harpactocoid copepods. Harpactocoid copepods were a less strongly selected and a less abundant prey than caprellid amphipods. However, the increase of this prey item in the diet of kelp bass also improved its diet quality and population size. Whereas the harvesting of both large rock wrasse and blackeye goby involved both of these prey, the harvesting of large rock wrasse had stronger impact on caprellid amphipods and the harvesting of blackeye goby had stronger impact on harpactocoid copepods. Garibaldi exhibited substantial increases in dietary quality and population size (15%, 8%, Table 53) not directly from these two prey, but from a secondary effect. Opaleye, strongly selective for harpactocoid copepods, increased its diet portion of this prey with multispecies harvesting and in turn decreased its dietary portion of other prey including algae and bryozoa (Table 52). Due to this increased availability of algae and bryozoa, Garibaldi, strongly selective for these prey, increased its consumption of them (Table 53), resulting in an increase in

Table 58. Diet volume of prey in percent by taxonomic group for the diet of kelp bass, Paralabrax clathratus, from the deterministic model for the four harvesting regimes.

	Harvesting Regime			
	No Harves- -ting	Single Spec.	Status Quo	Multi Spec.
Fish	1.57	1.51	1.48	1.03
Fish eggs	0.05	0.04	0.04	0.03
Algae	0.01	0.01	0.01	0.01
Hydrozoa	0.09	0.09	0.10	0.07
Polychaeta	0.09	0.10	0.17	0.10
Ostracoda	9.44	9.06	8.91	6.18
Calanoida	0.48	0.46	0.45	0.33
Harpacticoida	17.91	18.22	18.00	34.23
Mysidacea	6.42	6.15	6.06	4.19
Cumacea	0.11	0.11	0.10	0.07
Tanaidacea	25.34	25.04	24.76	20.38
Isopoda	3.17	3.08	3.06	2.17
Gammaridea	16.09	15.63	15.57	6.76
Caprellidea	17.73	18.77	19.21	23.05
Reptantia	0.29	0.31	0.58	0.23
Natantia	1.22	1.43	1.47	1.18
Ophiuroidea	0.00	0.00	0.00	0.00
Diet quality	10.58	10.68	10.65	13.26
Pop. size	1.03	0.45	0.45	0.52
Catch	-	0.19	0.19	0.24

Table 59. Diet volume of prey in percent by taxonomic group for the diet of rock wrasse (lg., >150 mm), Halichoeres semicinctus, from the deterministic model for the four harvesting regimes.

	Harvesting Regime			
	No Harves- -ting	Single Spec.	Status Quo	Multi Spec.
Fish eggs	0.13	0.12	0.12	0.09
Algae	1.19	1.17	1.22	0.98
Foraminifera	0.44	0.42	0.42	0.33
Porifera	0.45	0.43	0.43	0.33
Hydrozoa	0.02	0.02	0.02	0.02
Nemertea	0.46	0.44	0.43	0.32
Polychaeta	0.22	0.23	0.41	0.25
Polyplacophora	0.02	0.02	0.02	0.01
Gastropoda	0.37	0.38	0.99	0.29
Bivalvia	0.21	0.21	0.45	0.14
Pycnogonida	0.08	0.07	0.07	0.05
Ostracoda	0.26	0.25	0.24	0.18
Harpacticoida	11.38	11.62	11.32	23.41
Cirripedia	0.30	0.28	0.28	0.21
Mysidacea	0.27	0.26	0.25	0.19
Cumacea	0.21	0.20	0.19	0.15
Tanaidacea	14.26	14.08	13.72	12.26
Isopoda	3.76	3.63	3.55	2.73
Gammaridea	28.74	27.74	27.25	12.80
Caprellidea	27.79	29.34	29.59	38.49
Reptantia	0.20	0.21	0.38	0.17
Natantia	0.29	0.34	0.35	0.30
Bryozoa	7.90	7.52	7.18	5.53
Asteroidea	0.02	0.02	0.02	0.01
Ophiuroidea	0.14	0.14	0.23	0.14
Echinoidea	0.02	0.02	0.05	0.02
Ascidacea	0.90	0.85	0.83	0.62
Diet quality	6.74	6.87	6.87	8.48
Pop. size	6.42	6.50	6.40	4.65
Catch	-	-	0.06	2.64

Table 60. Diet volume of prey in percent by taxonomic group for the diet of *senorita* (sm., <150 mm), *Oxyjulis californica*, from the deterministic model for the four harvesting regimes.

	Harvesting Regime			
	No Harves- -ting	Single Spec.	Status Quo	Multi Spec.
Fish eggs	0.01	0.01	0.01	0.00
Algae	1.91	1.90	2.01	1.91
Porifera	0.00	0.00	0.00	0.00
Hydrozoa	0.68	0.69	0.74	0.66
Polychaeta	0.59	0.63	1.13	0.80
Gastropoda	0.04	0.04	0.12	0.04
Veleger	0.08	0.07	0.07	0.06
Bivalvia	0.04	0.04	0.10	0.04
Pycnogonida	0.00	0.00	0.00	0.00
Cladocera	0.00	0.00	0.00	0.00
Ostracoda	0.05	0.05	0.05	0.04
Calanoida	16.98	16.48	16.14	14.97
Harpacticoida	0.58	0.60	0.59	1.47
Cyclopoida	0.70	0.68	0.67	0.59
Caligoida	0.38	0.36	0.36	0.32
Cirripedia	0.76	0.74	0.74	0.65
Tanaidacea	0.32	0.32	0.32	0.34
Isopoda	12.84	12.60	12.47	11.40
Gammaridea	24.57	24.11	23.93	13.34
Caprellidea	23.26	24.96	25.44	39.46
Euphausiacea	0.01	0.01	0.01	0.01
Natantia	0.03	0.04	0.04	0.04
Insecta	0.02	0.02	0.02	0.01
Bryozoa	16.14	15.62	15.07	13.82
Ophiuroidea	0.00	0.00	0.00	0.00
Echinoidea	0.00	0.00	0.00	0.00
Diet quality	9.42	9.47	9.45	10.37
Pop. size	14.85	14.89	14.85	15.72
Catch	-	-	-	-

dietary quality and population levels. The impact of harpactocoid copepods released due to multispecies harvesting was limited since only kelp bass and opaleye were strongly selective of this prey.

Fishes that did not exhibit substantial gain in dietary quality and population size were: opaleye (diet quality 8%, population size 2%, Table 52), pile perch (3%, 0%, Table 54), black perch (3%, 2%, Table 61), small rock wrasse (2%, 1%, Table 62), large seniorita (-0.04%, -0.02%, Table 63), small sheephead (0.03%, 0.02%, Table 64), large sheephead (6%, 0%, Table 55), spotted kelpfish (-0.03, 0%, Table 65) and blackeye goby (4%, 2%, Table 66). These were fishes which were not highly selective for caprellid amphipods or harpactocoid copepods. All of these species except pile perch had increases in caprellid amphipods in their diet. These fishes would have been dietary losers except for secondary effects coming from the increase in the availability of other prey of high selective value. Black perch nearly doubled its dietary volume of caprellid amphipods which would have substantially decreased its dietary quality and population size (Table 61). However it also increased its dietary volume of prey of high selectivity value, tanaids by over 30% and therefore ended up with a small net increase in both dietary quality and population size. Small rock wrasse also doubled its dietary volume of caprellid amphipods, but increased its dietary volume of ostracoda, natantian decapods and bryozoa resulting in a small net increase of dietary quality and population size (Table 62). Similar secondary feeding effects were observed for small sheephead (Table 64), large sheephead

Table 61. Diet volume of prey in percent by taxonomic group for the diet of black perch, Embiotoca jacksoni, from the deterministic model for the four harvesting regimes.

	Harvesting Regime			
	No Harves- -ting	Single Spec.	Status Quo	Multi Spec.
Algae	0.10	0.10	0.11	0.12
Foraminifera	1.47	1.45	1.46	1.69
Porifera	0.00	0.00	0.00	0.00
Hydrozoa	0.57	0.59	0.63	0.70
Polychaeta	0.13	0.14	0.26	0.23
Polyplacophora	0.00	0.00	0.00	0.00
Gastropoda	0.20	0.21	0.55	0.23
Bivalvia	0.03	0.03	0.07	0.03
Ostracoda	1.65	1.61	1.58	1.73
Harpacticoida	0.12	0.12	0.12	0.36
Cyclopoida	0.31	0.30	0.29	0.32
Mysidacea	0.49	0.48	0.47	0.52
Cumacea	0.71	0.69	0.68	0.74
Tanaidacea	27.67	27.90	27.49	35.95
Isopoda	2.27	2.24	2.22	2.50
Gammaridea	54.94	54.20	53.85	37.06
Caprellidea	7.51	8.10	8.26	15.72
Reptantia	0.08	0.09	0.17	0.11
Natantia	0.19	0.23	0.24	0.30
Bryozoa	0.40	0.39	0.37	0.42
Ophiuroidea	0.09	0.09	0.15	0.13
Echinoidea	0.01	0.01	0.03	0.01
Ascidacea	1.07	1.04	1.02	1.12
Entoprocta	0.00	0.00	0.00	0.00
Diet quality	9.32	9.32	9.27	9.57
Pop. size	2.51	2.51	2.04	2.56
Catch	-	-	0.25	-

Table 62. Diet volume of prey in percent by taxonomic group for the diet of rock wrasse (sm., <150 mm), Halichoeres semicinctus, from the deterministic model for the four harvesting regimes.

	Harvesting Regime			
	No Harves- -ting	Single Spec.	Status Quo	Multi Spec.
Fish eggs	0.00	0.00	0.00	0.00
Algae	0.05	0.05	0.06	0.07
Hydrozoa	0.11	0.12	0.12	0.13
Polychaeta	0.23	0.25	0.45	0.39
Gastropoda	0.25	0.26	0.70	0.29
Bivalvia	0.21	0.21	0.45	0.20
Pycnogonida	0.01	0.01	0.01	0.01
Ostracoda	27.65	27.13	26.50	28.60
Cirripedia	0.03	0.03	0.03	0.03
Cumacea	0.21	0.21	0.20	0.22
Tanaidacea	2.49	2.52	2.48	3.17
Isopoda	3.90	3.86	3.81	4.21
Gammaridea	42.57	42.20	41.76	28.13
Caprellidea	10.85	11.76	11.94	22.21
Reptantia	0.38	0.41	0.76	0.47
Natantia	0.65	0.79	0.81	1.00
Bryozoa	9.13	8.92	8.58	9.47
Ophiuroidea	0.16	0.17	0.27	0.23
Ascidacea	1.12	1.10	1.07	1.15
Diet quality	9.28	9.22	9.14	9.40
Pop. size	1.98	1.97	1.96	2.00
Catch	-	-	-	-

Table 63. Diet volume of prey in percent by taxonomic group for the diet of senorita (lg., >150 mm), Oxyjulis californica, from the deterministic model for the four harvesting regimes.

	Harvesting Regime			
	No Harves- -ting	Single Spec.	Status Quo	Multi Spec.
Fish eggs	0.01	0.01	0.01	0.01
Algae	4.32	4.37	4.59	4.50
Polychaeta	0.81	0.87	0.57	1.15
Polyplacophora	0.02	0.02	0.02	0.02
Gastropoda	0.42	0.43	0.15	0.41
Bivalvia	0.02	0.02	0.04	0.02
Cladocera	0.08	0.08	0.08	0.07
Ostracoda	0.05	0.05	0.04	0.04
Calanoida	46.65	45.93	44.88	42.66
Harpacticoida	1.75	1.84	1.81	4.59
Cyclopoida	2.78	2.72	2.66	2.42
Caligoida	0.15	0.14	0.14	0.13
Mysidacea	0.01	0.01	0.01	0.01
Isopoda	2.28	2.27	2.24	2.10
Gammaridea	11.15	11.10	10.99	6.29
Caprellidea	10.57	11.51	11.69	18.64
Natantia	0.01	0.01	0.02	0.02
Bryozoa	18.43	18.09	17.41	16.42
Ophiuroidea	0.19	0.20	0.33	0.24
Echinoidea	0.00	0.00	0.01	0.00
Ascidacea	0.31	0.30	0.29	0.27
Diet quality	13.17	13.04	12.89	12.54
Pop. size	10.23	10.17	9.99	9.93
Catch	-	-	0.10	-

Table 64. Diet volume of prey in percent by taxonomic group for the diet of sheephead (sm., <150 mm), Semicossyphus pulcher, from the deterministic model for the four harvesting regimes.

	Harvesting Regime			
	No Harves- -ting	Single Spec.	Status Quo	Multi Spec.
Fish eggs	0.10	0.10	0.09	0.11
Nemertea	1.13	1.11	1.08	1.27
Polychaeta	0.63	0.69	1.25	1.18
Polyplacophora	0.00	0.00	0.00	0.00
Gastropoda	0.30	0.31	0.84	0.37
Bivalvia	0.26	0.26	0.56	0.27
Ostracoda	13.13	12.97	12.64	14.94
Cyclopoida	16.21	15.93	15.52	18.32
Caligoida	0.00	0.00	0.00	0.00
Tanaidacea	14.49	14.78	14.49	20.39
Isopoda	4.09	4.09	4.03	4.89
Gammaridea	48.11	48.03	47.44	35.14
Caprellidea	0.95	1.04	1.06	2.18
Reptantia	0.23	0.26	0.48	0.32
Natantia	0.28	0.34	0.35	0.48
Ophiuroidea	0.05	0.06	0.10	0.09
Echinoidea	0.03	0.03	0.07	0.04
Diet quality	7.49	7.46	7.43	7.70
Pop. size	2.27	2.26	2.26	2.31
Catch	-	-	-	-

Table 65. Diet volume of prey in percent by taxonomic group for the diet of spotted kelpfish, Gibbonsia elegans, from the deterministic model for the four harvesting regimes.

	Harvesting Regime			
	No Harves- -ting	Single Spec.	Status Quo	Multi Spec.
Fish	0.03	0.03	0.03	0.04
Fish eggs	0.00	0.00	0.00	0.00
Algae	0.24	0.24	0.25	0.33
Foraminifera	4.01	3.95	3.98	5.06
Polychaeta	0.10	0.10	0.19	0.18
Gastropoda	0.06	0.06	0.17	0.08
Cladocera	0.01	0.01	0.01	0.01
Ostracoda	0.24	0.23	0.23	0.28
Calanoida	0.20	0.20	0.20	0.25
Cirripedia	0.03	0.03	0.03	0.04
Isopoda	16.15	16.00	15.83	19.68
Gammaridea	69.06	68.40	67.89	51.45
Caprellidea	9.30	10.09	10.31	21.69
Reptantia	0.22	0.24	0.44	0.31
Natantia	0.35	0.43	0.44	0.62
Diet quality	15.48	15.40	15.35	14.95
Pop. size	0.17	0.17	0.17	0.17
Catch	-	-	-	-

Table 66. Diet volume of prey in percent by taxonomic group for the diet of blackeye goby, Coryphopterus nicholsii, from the deterministic model for the four harvesting regimes.

	Harvesting Regime			
	No Harves- -ting	Single Spec.	Status Quo	Multi Spec.
Fish	0.03	0.03	0.02	0.02
Fish eggs	0.00	0.00	0.00	0.00
Algae	0.66	0.66	0.70	0.72
Foraminifera	3.07	3.03	3.04	3.09
Porifera	0.13	0.12	0.12	0.12
Nemertea	0.09	0.09	0.08	0.08
Polychaeta	0.64	0.70	0.27	0.98
Polyplacophora	0.01	0.01	0.01	0.01
Gastropoda	0.38	0.39	1.07	0.39
Bivalvia	0.07	0.07	0.15	0.06
Pycnogonida	0.23	0.22	0.21	0.21
Ostracoda	3.90	3.83	3.73	3.61
Calanoida	22.62	22.18	21.63	21.85
Harpacticoida	1.82	1.91	1.87	5.02
Cyclopoida	2.18	2.13	2.07	2.00
Cumacea	4.00	3.90	3.80	3.68
Tanaidacea	27.96	28.31	27.75	32.02
Isopoda	4.45	4.41	4.35	4.33
Gammaridea	23.01	22.81	22.58	13.69
Caprellidea	3.51	3.81	3.88	6.55
Reptantia	0.14	0.16	0.29	0.16
Natantia	0.71	0.86	0.89	1.00
Bryozoa	0.27	0.26	0.25	0.25
Ophiuroidea	0.11	0.12	0.19	0.15
Echinoidea	0.01	0.01	0.02	0.01
Diet quality	6.80	6.82	6.78	7.12
Pop. size	7.52	7.53	7.51	4.80
Catch	-	-	-	2.87

(Table 55) and blackeye goby (Table 66). The most dramatic example of secondary feeding effects was pile perch (Table 54) which did not feed on either caprellid amphipods or harpactocoid copepods, but increased its dietary quality and population size because of increased consumption of gastropods and ophiroids. These prey's availability were increased due to other fishes (principally large sheephead) switching to caprellid amphipods and harpactocoid copepods.

All three models: static, stochastic and deterministic, targeted the same three fishes for their multispecies harvesting regime: large rock wrasse, island kelpfish and blackeye goby. The difference between the deterministic model and the two previous models was the order in which the fishes were added to the multispecies harvesting regime. As in the stochastic model, three runs were made in which kelp bass and one of these three fishes were harvested (1) kelp bass and large rock wrasse, 2) kelp bass and island kelpfish and 3) kelp bass and blackeye goby; all at a mortality of $F=0.38$) to establish how effective alternate harvesting regimes would be at increasing catch of kelp bass (the management goal). For reference, catch from single species harvesting (kelp bass $F=0.38$) was 0.191 individuals/year and from multispecies harvesting (kelp bass, large rock wrasse $F=0.38$ and blackeye goby $F=0.76$) was 0.242 individuals/year. Harvesting of large rock wrasse (the first step in the multispecies harvesting regime) resulted in a catch of 0.225 individuals/year, an increase of 18% over single species harvesting. Harvesting of island kelpfish, the second alternate

harvesting regime, yielded a catch of 0.220 individuals/year, an increase of 15%. The third alternate harvesting regime, harvesting of blackeye goby, had a catch of 0.212 individuals/year, an increase of 11%. In contrast to the stochastic model where one alternate harvesting regime was clear superior to the others, two of the alternate harvesting regimes were close in their level of effectiveness (18% vs 15%) in terms of increasing catch of kelp bass. As in the stochastic model, the order that fish species were added to the multispecies harvesting regime was different than the order of effectiveness found here.

In the deterministic model unlike the stochastic model, the changes in kelp bass populations were very different under the four harvesting regimes (Figure 5). Kelp bass under the no harvesting regime had an increasing population size from initial conditions to a much larger equilibrium population size than in the stochastic model. Under the single species and status quo harvesting, kelp bass populations had virtually identical behaviors. Here, kelp bass populations gradually decreased to population sizes that were near to those in the stochastic model. Kelp bass populations under the multispecies harvesting also initially decreased, but then increased gradually to a level near that of the stochastic multispecies harvesting. Under the no harvesting regime, the kelp bass population sizes are much higher in the deterministic model than in the stochastic model. However under the other three harvesting regimes, the population sizes of the two models are similar. The differences in population sizes between no harvesting and the other three harvesting regimes were

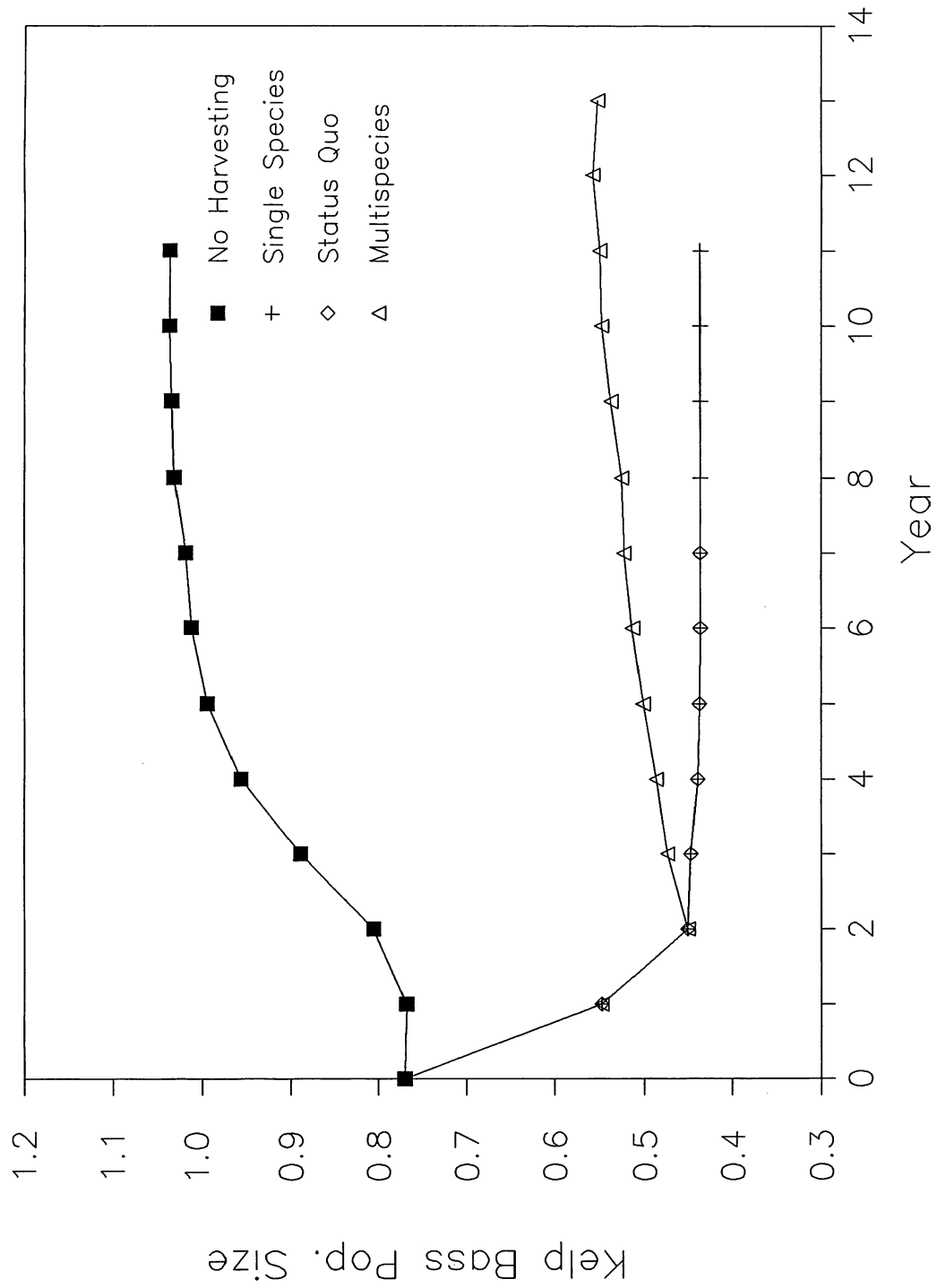


Figure 5. Kelp bass population sizes from the deterministic model under the four harvesting regimes (no harvesting, single species, status quo and multispecies harvesting).

much greater in the deterministic model than in the stochastic model. This accounts for the increased catch of kelp bass in the deterministic model.

DISCUSSION

The impact of multispecies harvesting on the entire community can be broken down into a group of fishes that had substantially improved population size (dietary winners) and those that remain neutral or had only small increases or decreases. Between the two model structures (stochastic and deterministic), there is no overlap between the fishes that were dietary winners except for kelp bass (which was the goal of multispecies harvesting) and island kelpfish. The difference between dietary winners reflects the different key prey through which multispecies harvesting was successful. The dietary winners in the stochastic model (kelp bass, small rock wrasse, island kelpfish and blackeye goby) all had strong selectivities for the two decapod groups; while the dietary winners in the deterministic model (painted greenling, kelp bass, Garibaldi, large rock wrasse, small senorita, and island kelpfish) mostly had strong selectivity for caprellid amphipods. In the deterministic model, there was some secondary effects where dietary shifts from nonharvested fishes released prey that in turn improved the diet and population size of other fishes.

Previous multispecies modeling studies have often investigated model behavior and pointed out areas where substantial improvement in catch of target fishes would occur through multispecies management (Parrish 1975, Anderson and Ursin 1977, Dunn 1979, May et al 1979 and Overholtz and Tyler 1986). The closest that these studies have come to a prediction of improvement resulting from multispecies management is the

forecast that reduction of marine mammals in the Bering Sea would increase fin fish catch several times (Laevastu and Larkin 1981). In this study, multispecies harvesting increased target catch by 19 to 26 percent. In this complex of fishes, there was no direct predatory links; while in several of the models above, there is direct predation by one fish on the juvenile stages of other fishes. These situations of direct predation would lead to much larger gains from multispecies management. Improvement in catch of target fishes from multispecies harvesting may also be higher when the target fish is more heavily stressed.

CONSTRUCTION OF MULTISPECIES MANAGEMENT PLANS AND KEY PREY

Ultimately multispecies management regimes from communities where members are not directly preying on each other, will have to depend on the transfer of trophic resources from non-target species to target species to be success. The way this was done in the construction of multispecies management regimes for the different model structures was to calculate the impact of the target species feeding on the diet of each of the non-target species and calculating the change in population size of the target species under initial conditions. This change was then multiplied by the non-target species population. The non-target species whose diet resulted in the largest population size of the target species was selected and model runs were made over a range of fishing mortalities on the selected non-target species. The model runs over an increasing range of fishing mortalities resulted in target species population sizes increasing to an

asymptote and the lowest mortality which produced the asymptotic population size was chosen. This process then went through another iteration using the new diets of the non-target species and another non-target species was added to the multispecies management regime in a stepwise fashion. These iteration continued until the population size of the target species increased by less than five percent and the process was stopped with addition of the previous species.

In both models, the transfer of trophic resources from non-target species to target species occurs largely through certain key prey and these key prey are the mechanism through which multispecies harvesting works. In the stochastic model, these key prey were the decapod prey groups; while in the deterministic model, they were caprellid amphipods and harpacticod copepods. In both models, the increase in diet quality from these key prey were at least equal to 80% of the total diet quality increase, so the increase in diet quality, and therefore reproduction, came substantially from the redistribution of these key prey.

The concept of key prey is related to Paine's (1969) concept of a keystone species. Paine defines a keystone species as one which has a disproportionately large impact of community activities. Paine expressed the concept generally, but was referring to predators which enhance community stability and species diversity through non-selective predation. Key prey are prey which have impact on the diet of predator out of proportion to their numbers. The differences between the two concepts are

1) that the impact is on the next level of organization, the population, rather than the community level and 2) the impact of key prey is upward in the trophic web rather than downward as in Paine's keystone predator.

These key prey are also important in the diet quality of fish in nature. Overall diet quality of 110 kelp bass was plotted versus the diet quality due to these key prey (Figure 6). While there is more variation than in the model results, there is a strong positive trend of increasing diet quality with increasing amounts of key prey (linear regression ANOVA $F=234.88$; d.f. = 1,108; $P < 0.001$). In nature, changes in key prey are then largely responsible for changes in overall diet quality of kelp bass which supports the model results that key prey are the mechanism through which multispecies management works.

These key prey as a "quick and dirty" alternative method of construction of multispecies management regimes present a practical reduction in the complexity of constructing these regimes. In the model, prey densities, fish populations sizes and feeding selectivities are very accurate and even the reproductive coefficients have ballpark accuracy, but this is because the Santa Catalina fish community is a very small, limited system which is easily studied. For larger systems, estimating these parameters is more difficult. As an example, Anderson and Ursin (1977) estimate the feeding selectivity of cod feeding on herring at a low value because herring are fast swimmers and a schooling fish. An alternative approach to constructing multispecies regimes is based on these key prey. Candidates that may be key prey could be identified from gut content studies on the target

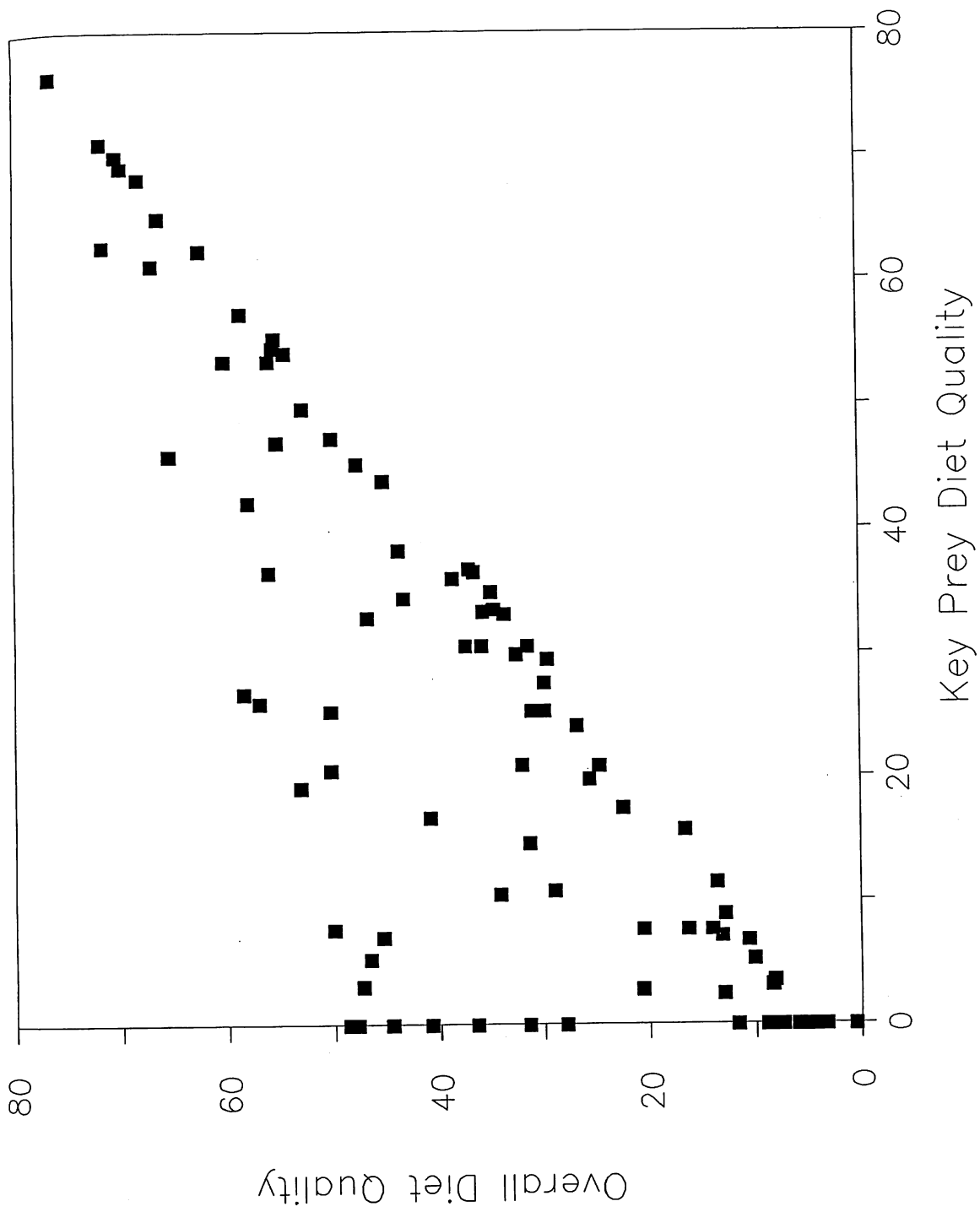


Figure 6. Key prey diet quality plotted versus overall diet quality for kelp bass (n = 110) from nearshore Catalina Island.

fish species. After this list is created, the importance of different prey could be ranked by fine-scale studies of both gut contents of the target fish species and occurrence of these prey. Once these key prey are ranked, gut content studies for co-occurring fishes could determine if these key prey are mutually important with other fish predators. Then the greatest benefit would be through studies of the key prey themselves.

Reproductive characteristics, time-area variation of these key prey will control the ability to successfully develop a multispecies harvesting regime.

The limitations of this approach are 1) that it focuses only on the target species, 2) it is not comprehensive in the sense that it considers all possible solutions and 3) that the recommendations resulting from this approach are qualitative rather than quantitative. All of these problems can be substantial. Focusing only on the target species can have substantial and unexpected impact on other fishes from the multispecies harvesting. When secondary effects are important or where more than one fish is the target of the fishery, these impacts can be very important. The second problem, lack of a comprehensive solution, can be important in situations where combinations of prey would have greater impact than a single one. The problem of qualitative recommendations is one of credibility. Qualitative suggestions about how to manage fisheries are regarded as lacking the authority that numerical based suggestions appear to have. This increases the difficulty of gaining acceptance of a proposed management measure.

MULTISPECIES HARVESTING AND ECOLOGICAL THEORY

The impact of harvesting in terms of ecological theory is dealt with by a pair of hypothesis, the niche compression hypothesis and competitive or ecological release. The result of the combination of these hypothesis is often called species packing. The niche compression hypothesis (MacArthur and Wilson 1967, Pianka 1974) states that animals, when faced with more intense competition from other species, will restrict their utilization of shared resources. This hypothesis is usually stated in terms of trophic resources and says that as competition increases, species will feed less heavily on diet items that are used by both species. The result is a decrease in feeding overlap. Competitive or ecological release is the opposite situation. It is a descriptive term that has come into use and has no clear source. It is the expansion of niches, again usually trophic, under the reduction of interspecific competition. So when interspecific competition is reduced, animals would increase feeding on diet items that are used by both species and increase diet overlap. Both of these concepts are an integral part of a set of ecological theory based largely on competition (MacArthur 1972).

The prime example of the operation of these concepts is Zaret and Rand's (1971) study of tropical stream fish. This is an often cited example of species-packing and these two concepts in operation. Their study is of nine species of fish in tropical streams that experience a dry and wet season. The nine species change from very small dietary overlap (narrow distinct food

niches) during the dry season to large dietary overlap (widely-overlapping food niches) during the wet season. Prey abundances, measured independently, are at a low during the dry season and are very abundant during the wet season. This is interpreted as the operation of these concepts. As food abundance decreases during the dry season, interspecific competition increases, trophic niches compress away from prey used by both species and diet overlap decreases. When food abundance increases during the wet season, interspecific competition decreases, competitive releases occurs, feeding on prey used by both species increases and diet overlap increases. While problems with arguments using patterns of overlap to infer competition are recognized (Colwell and Futuyma 1971, Hulbert 1978 and Abrams 1980), diet overlap is still widely used to estimate one species impact on another (Larson 1972, Bray and Ebeling 1975, Obrebski and Silbert 1976, Laur and Ebeling 1981). Others use overlap patterns after they have tested for a significant difference between mean overlap versus the mean overlap of 50 randomly generated competition-free communities from Sale (1974). Then significantly different overlap are used to infer impact of one species on another (Gadfeller and Johnson 1983). So patterns of dietary overlap are still widely used to infer the strength of interspecies relationships.

Multispecies management would operate through the processes described by these concepts and they predict that harvesting would promote larger dietary overlap. Harvesting constitutes an increase in mortality on the target species. This decrease in

population size would also result in a decrease in resource utilization. The resources, in this case trophic, not utilized would have the same impact as competition release and accompanying this competitive release, dietary overlap should increase. The principles operating here are the same as in the Zaret and Rand study only the increase in food is coming from reduced population size due to harvesting rather than the seasonality of the environment. These arguments are developed more rigorously for the case where mortality is caused by a natural predator rather than a fishery by Roughgarden and Feldman (1975) and Vance (1978).

The response of dietary overlap indices to harvesting calculated from model results do not follow the prediction of increasing overlap in response to harvesting and in fact, are mixed between increasing and decreasing with increased harvesting. Using the index suggested by Schoener (1971), dietary overlap values are calculated for the four fish species involved in multispecies harvesting; kelp bass, large rock wrasse, island kelpfish and blackeye goby; for four harvesting regimes; stochastic single species and multispecies harvesting and deterministic single species and multispecies harvesting. The prediction from the theory is that with increased harvesting (and decreased population size) multispecies harvesting food niches should widen from single species harvesting food niches and diet overlap should increase. In fact, the change in the overlap index is mixed. There are six pairs of overlap indices for each of the stochastic and deterministic model, twelve in all. Of those twelve, three did not change, four increased in

diet overlap from single species to multispecies harvesting and five decreased in diet overlap (Table 67). Dietary overlap did not respond in any consistent manor to the release of resources accompanying increased harvesting.

While in the simplest and most straightforward case, these concepts of niche compression, competitive release and species-packing are accurate and representative; as situations become more complex, they often become distorted by patterns of abundance and selectivity and these concepts lose their descriptive power. In the model results, there are large numbers of gammarid amphipods, a prey not highly selected by any of these four fishes. In single species harvesting, feeding on gammarids makes up a significant amount of dietary overlap. In multispecies harvesting, overlap due to gammarid amphipods decreases in every case. In some cases, this is offset by increases in dietary overlap from larger amounts of rarer key prey; however in other cases, this does not occur. This accounts for the mixed response of diet overlaps from the model studies. In the model studies as key prey are less abundant, the predators do not shift to prey that used solely by that predator, but to a prey which is taken by all of the predators, but only at low selectivity.

The differences between theoretical predictions and the results of this model study are important not only in the theoretical sense, but also because what general advice there is on management of multispecies complexes has its base in the same set of theory. The advice for dealing with a situation where two

Table 67: Testing the Niche Compression hypothesis; The change in the Schoender diet overlap index for four species of fish; kelp bass, large rock wrasse, island kelpfish and blackeye goby; from single species and multispecies harvesting for both the stochastic and deterministic models.

Stochastic Model

Single Species

	Kelp Bass	Rock Wrasse (lg.)	Island Kelpfish	Blackeye Goby
Kelp Bass	1.000	0.588	0.631	0.394
Rock Wrasse (lg.)		1.000	0.538	0.631
Island Kelp			1.000	0.354
Blackeye goby				1.000

Multispecies

	Kelp Bass	Rock Wrasse (lg.)	Island Kelpfish	Blackeye Goby
Kelp Bass	1.000	0.582	0.666	0.432
Rock Wrasse (lg.)		1.000	0.538	0.630
Island Kelp			1.000	0.386
Blackeye goby				1.000

Deterministic Model

Single Species

	Kelp Bass	Rock Wrasse (lg.)	Island Kelpfish	Blackeye Goby
Kelp Bass	1.000	0.644	0.420	0.548
Rock Wrasse (lg.)		1.000	0.634	0.496
Island Kelp			1.000	0.358
Blackeye goby				1.000

Multispecies

	Kelp Bass	Rock Wrasse (lg.)	Island Kelpfish	Blackeye Goby
Kelp Bass	1.000	0.687	0.376	0.462
Rock Wrasse (lg.)		1.000	0.586	0.424
Island Kelp			1.000	0.308
Blackeye goby				1.000

or more species are feeding on the same prey is almost always based on the Lotka-Volterra equation. These equations play a central role in the development of a competition based ecological theory and are so intimately connected to this theory as to be essentially the same thing. Most multispecies harvesting modeling efforts based on the Lotka-Volterra equations reflect direct competition in which one fish species impacts another directly (Larkin 1963, 1966; Clark 1976; Pope 1976, 1979; FAO 1979; Kirkwood 1982). Other attempts do explicitly include indirect effects and specifically model prey populations (May et al 1979) as do the models used here. The May et al study is based on an Antarctic ecosystem of whales, seals and krill. The recommendations are essentially an estimation of the amount of krill released through competitive release, the changes in species packing due to harvesting and an allocation of that release to the fishery. Through analogy, these recommendations are extended to the North Sea Fisheries. While again in their simplest case, these patterns of resource reallocations are appropriate; as complexity increases as it does in real world situations (whales and seals fed on other prey besides krill), these patterns may become convoluted and unpredictable. These kinds of problems leave little hope for any sort of overall or generalized advice on management of multispecies complexes.

COMPARISON OF STOCHASTIC AND DETERMINISTIC MODELS

Increases in catch of kelp bass were in the same range for the stochastic (15%) and deterministic (26%) models in response to multispecies harvesting, but there were major differences in

their behavior. In this case, the deterministic model does not represent "average" behavior of the stochastic model.

Multispecies harvesting in the stochastic model resulted in a smaller improvement in kelp bass catch than in the deterministic model and required high mortalities to do so. The same complex of fishes were involved in multispecies harvesting in both models, but the order of their importance to the harvesting regimes is reversed. Alternative harvesting regimes for the stochastic model were not close to being as effective in increasing kelp bass catch as the first step of the multispecies regime; while in the deterministic model, the alternative regimes were much closer in effectiveness to the multispecies regime. Finally the key prey through which trophic resources were transferred were different in the two models.

The question of whether a stochastic or deterministic model is more appropriate depends on the system being modeled and what tasks the model is expected to accomplish. The construction of a deterministic model is a very data-intensive process and the construction of a stochastic model is even more so. In many instances, the data is just not available for formulation and parameter estimation of a stochastic model. This is particularly true for larger systems such as the Bering Sea or the North Sea where actual management efforts using these types of models are being attempted. Also with simpler deterministic models, powerful tools for analyzing model behavior are available. Even if using these analytical methods is not possible, deterministic models are cheaper and faster to run on computers. This can be a

factor where stochastic models require 20 to 30 run each taking several hours. The justification for using stochastic models comes from the amount of variation in the data that is characteristic of investigating trophic interactions. This variability is a real part of the biological organization and needs to be represented in the modeling process. While deterministic models seem to be more pragmatic, stochastic models incorporate the variation that is a real part of these processes.

The stochastic model had differences in behavior from the deterministic model which were due to the continuous variation in diet selection from its feeding submodel. The stochastic model used here showed more resilience to change from the impacts of harvesting than the deterministic model. The increase in catch of kelp bass in the deterministic model was roughly double that of the stochastic model and this was with lower fishing mortalities in the deterministic model's multispecies harvesting regime. There were also secondary changes in diet of fishes not directly harvested in the deterministic model, but not in the stochastic model. This increased 'buffering' in the stochastic model results from the continuous fluctuations in diet selection versus the fixed diet selection of the deterministic model. It may be that the continuous fluctuation in diet selection in nature also produces some compensatory effect. The other area of difference in model behavior was the distribution of kelp bass population sizes at equilibrium, rather than the point estimate from the deterministic model. In the stochastic single species harvesting regime, the kelp bass population sizes when divided into two groups, showed different paths to equilibrium

populations. These two equilibrium populations were significantly different only at a 10% level. This raises the question of dealing with forecasts resulting in a distribution and even though it did not occur in this study, stochastic models may have multiple outcomes from the same initial conditions.

Life History Patterns in Marine Fishes and Their Consequences for Management

Introduction

The ecological and genetic properties of a species are intimately linked. The morphological and reproductive characteristics, population sizes and genetic frequencies of species are adjusted to their environments by natural selection. Species inhabiting different environments show different patterns of life history characteristics. The relationship among habitat, ecological strategies and population parameters has been termed *r* and *K* selection (MacArthur and Wilson 1967) and/or optimal life histories (Gadgil and Bossert 1970). This body of theory is based on the assumption that natural selection operates on these characteristics to maximize the number of surviving offspring produced. Under an environmental regime with a large component of unpredictable, nonselective, mortality an organism will allocate a larger portion of its resources to reproductive activities (an *r* strategist). Conversely the optimal allocation of resources for a population subjected to a high proportion of predictable selective mortality will be toward increasing individual fitness frequently through competitive ability (a *K* strategist). With the number and variability of factors operating on any particular species, no species is going to be an *r* or *K* strategist in absolute sense. A species will only occupy a relative position on the *r* and *K* continuum.

In fisheries biology, the value of comparative studies of life history parameters has long been recognized (Holt 1962;

Beverton 1963; Cushing 1971; Alverson and Carney 1975). These life history parameters should vary in a consistent pattern which can be predicted from the theory of r and K selection. In this paper, these predictions are tested with life history parameters from major groups of marine fishes. The theory has implications for management, particularly when fisheries are in the initial stages of development.

The Theory of r and K Selection

The theory of r and K selection is based on two assumptions about the allocation of a population's resources between competitive and reproductive functions (Pianka 1974; Gadgil and Bossert 1970; Schaffer and Gadgil 1975). The first is that there is a positive relationship between the amount of resources spent on an offspring and the fitness of that offspring. The second assumption is that any species only has a fixed amount of resources available. This results in an inverse relationship between the number of offspring produced and their average fitness. The criterion for success in natural selection is the number of surviving offspring that a parent produces (Crow and Kimura 1970). Therefore, the best reproductive strategy is a compromise between two conflicting demands: production of the largest possible total number of offspring (r selection) and production of offspring with the highest possible fitness (K selection). The particular point of compromise for any species will be a function of the selection factors operating on that species and would be that species' position on the r and K

continuum.

The second part of the theory concerns the relationship between these life history strategies and the habitat the species occupies (Southwood et al. 1974; Southwood and Comins 1976). If mortality factors in an environment are variable and/or unpredictable, then their effects are likely to be less selective in terms of population size or of the phenotype involved. Under these circumstances, individual competitive fitness is of relatively less importance. The best strategy would be to place maximal resources into reproduction and produce as many offspring as possible (r selection).

The contrasting situation is an environment in which mortality factors are stable and/or predictable. Mortality under these circumstances will result in strong selection for individual fitness and there will be pronounced differences between their effects on different phenotypes. In these stable environments, the optimal strategy would be to produce offspring with substantial competitive ability (K selection). Due to the previously assumed relationship between fitness per offspring and the number of offspring produced, this also means the production of fewer offspring.

The two situations described above are end points of a spectrum. Species will always have a number of different selective pressures operating on them, both spatially and temporally. This is particularly evident in aquatic organisms which characteristically go through several life history stages. This again emphasizes that the concept of r and K selection should be applied only in a comparative sense. Finally,

comparisons must be made between species of a similar ecological nature. Comparisons between species of different ecological types is meaningless since fundamentally different types of selective factors will be operating in those cases.

r and K Selection in Marine Fishes

Natural selection will favor nonreproductive activities at the expense of reproductive activities only when they enhance reproduction at later stages in the life history and thereby maximize overall survival (Crow and Kimura 1970). Changes in allocation of a species' resources from reproductive to competitive activities will only occur in habitats where competitive activities enhance the survival of future offspring. The result of this is that organism under different selection pressures will have characteristic life history patterns. An r selected species will have life history strategies which tend toward productivity. The K selected species will have life history strategies which tend toward efficient exploitation of a specific limiting resource (Pianka 1974). Therefore, specific combinations of population parameters can be identified as being characteristic of an r strategist, while the opposing combination would be characteristic of a K strategist.

A species which is exposed to a large component of nonselective or catastrophic mortality (i.e. an r strategist) would be selected for characteristics that would increase productivity. Increasing productivity through reproductive activity generally implies; 1) early maturity, 2) rapid growth

rates, 3) production of larger numbers of offspring at a given parental size and 4) maximum production of offspring at early age (Gadgil and Bossert 1970). Other characteristics which are result of the allocation of large portions of resources to reproductive activity are: 1) small body size, 2) high rates of mortality and 3) shorter life span (Pianka 1974; Gadgil and Solbring 1972). In terms of commonly measured population parameters in fishery biology, an r selected species would have: 1) a low age at first maturity, 2) a high value of k from the von Bertalanffy growth equation, 3) a small L_{∞} from the von Bertalanffy growth equation, 4) high rates on instantaneous mortality (M) and 5) low maximum age.

Even in environments with predictable mortality sources, increase allocation of resources to competitive activities will only occur when two prerequisites are met (Schaffer and Gadgil 1975). The first is that reproductive potential increase with some function of age. The second is that there is some additional mortality risk associated with reproduction. Under these assumptions, the attributes associated with a K strategist would be: 1) delayed maturity, 2) reduced growth rates, 3) low mortality rates, 4) large body size and 5) longer life span. Again in terms measured in fishery biology, a K selected species would have: 1) a high age at first maturity, 2) a low k from the von Bertalanffy growth equation, 3) a large L_{∞} from the von Bertalanffy growth equation, 4) a low instantaneous natural mortality (M) and 5) a high maximum age.

Using these life history correlates of r and K selection (summarized in Table 1), it is possible to predict the signs of a

Table 1. Summary of hypothetical r and K correlates in life history parameters of fishes.

Characteristics	r Selected	K Selected
Body size, L_{∞} ¹	Small	Large
Maximum age	Low	High
Age at first maturity	Low	High
Natural Mortality	High	Low
Growth rate, k ¹	High	Low

¹ The parameter from the von Bertalanffy growth equation was used to represent the actual characteristic.

correlation matrix between life history parameters (Table 2). The predicted matrix can be compared with actual matrices calculated using Spearman's rank correlation coefficient. This coefficient only assumes that the observed data are mutually independent and come from a continuous bivariate population (Hollander and Wolfe 1973).

Results

Life history parameters were gathered from the literature for several major groups of marine fishes. Often there were multiple sets of data for the same species from different locations. Each set of values was used as a separate data case. The literature citation for the actual parameters are listed by group in Appendix I. Correlation matrices were calculated for the following groups of fish: 1) herring and anchovies, Clupeidae and Engraulidae (Table 3), 2) salmons, Salmonidae (Table 4), 3) cods, Gadidae (Table 5), 4) rockfishes, Scorpaenidae, Genus Sebastes (Table 6), and 5) flatfishes, Pleuronectiformes (Table 7).

All of the observed correlations agree with the predicted correlations in sign (Table 8). Of the observed correlations, 40 of 46 (or 87%) were significantly different from zero at a 5% probability level. If the observed agreement of correlation coefficients were distributed randomly (i.e. p = probability of agreement = 0.5 and q = probability of disagreement = 0.5), then the number of agreements would follow a binomial distribution. The binomial test (Hollander and Wolfe 1973) can be used to test the hypothesis that the number of agreements between the

Table 2. Predicted signs of correlation matrix of life history parameters in fishes.

Characteristics	L_{∞}^1	Maximum age	Age at first maturity	M	k^1
Body size, L_{∞}^1	1.0	+	+	-	-
Maximum age		1.0	+	-	-
Age at first maturity			1.0	-	-
Natural Mortality, M				1.0	+
Growth rate, k^1					1.0

¹ The parameter from the von Bertalanffy growth equation was used to represent the actual characteristics.

Table 3. Correlation coefficients between life history parameters for herring and anchovies (family Clupeidae and Engraulidae). For sources of data see Appendix I. The number in parentheses represents the significance value for that particular coefficient since the number of data cases was different for each correlation.

Characteristics	L_{∞}^1	Maximum age	Age at first maturity	M	k^1
Body size, L_{∞}^1	1.0	0.846 (0.001)	0.816 (0.001)	-0.746 (0.001)	-0.720 (0.001)
Maximum age		1.0	0.904 (0.001)	-0.797 (0.001)	-0.763 (0.001)
Age at first maturity			1.0	-0.702 (0.001)	-0.732 (0.001)
Natural Mortality, M				1.0	0.876 (0.001)
Growth rate, k^1					1.0

¹ The parameter from the von Bertalanffy growth equation was used to represent the actual characteristics.

Table 4. Correlation coefficients between life history parameters for salmon (family Salmonidae). For sources of data see Appendix I. The number in parentheses represents the significance value for that particular coefficient since the number of data cases was different for each correlation.

Characteristics	L_{∞}^1	Maximum age	Age at first maturity	M	k^1
Body size, L_{∞}^1	1.0	0.765 (0.001)	0.728 (0.032)	-0.785 (0.001)	-0.730 (0.002)
Maximum age		1.0	0.776 (0.020)	-0.737 (0.003)	-0.674 (0.004)
Age at first maturity			1.0	-0.644 (0.084)	-0.812 (0.013)
Natural Mortality, M				1.0	0.896 (0.001)
Growth rate, k^1					1.0

¹ The parameter from the von Bertalanffy growth equation was used to represent the actual characteristics.

Table 5. Correlation coefficients between life history parameters for cods (family Gadidae). For sources of data see Appendix I. The number in parentheses represents the significance value for that particular coefficient since the number of data cases was different for each correlation.

Characteristics	L_{∞}^1	Maximum age	Age at first maturity	M	k^1
Body size, L_{∞}^1	1.0	0.795 (0.002)	0.833 (0.001)	-0.647 (0.022)	-0.666 (0.001)
Maximum age		1.0	0.737 (0.014)	-0.654 (0.028)	-0.702 (0.008)
Age at first maturity			1.0	-0.715 (0.084)	-0.658 (0.013)
Natural Mortality, M				1.0	0.950 (0.001)
Growth rate, k^1					1.0

¹ The parameter from the von Bertalanffy growth equation was used to represent the actual characteristics.

Table 6. Correlation coefficients between life history parameters for rockfishes (family Scorpaenidae, genus Sebastes). For sources of data see Appendix I. The number in parentheses represents the significance value for that particular coefficient since the number of data cases was different for each correlation.

Characteristics	L_{∞}^1	Maximum age	Age at first maturity	k^1
Body size, L_{∞}^1	1.0	0.662 (0.019)	0.456 (0.088)	-0.490 (0.075)
Maximum age		1.0	0.612 (0.030)	-0.567 (0.040)
Age at first maturity			1.0	-0.651 (0.021)
Growth rate, k^1				1.0

¹ The parameter from the von Bertalanffy growth equation was used to represent the actual characteristics.

Table 7. Correlation coefficients between life history parameters for flatfishes (order Pleuronectiformes). For sources of data see Appendix I. The number in parentheses represents the significance value for that particular coefficient since the number of data cases was different for each correlation.

Characteristics	L_{∞}^1	Maximum age	Age at first maturity	M	k^1
Body size, L_{∞}^1	1.0	0.755 (0.001)	0.956 (0.001)	-0.291 (0.156)	-0.619 (0.005)
Maximum age		1.0	0.824 (0.001)	-0.355 (0.142)	-0.808 (0.001)
Age at first maturity			1.0	-0.630 (0.014)	-0.732 (0.001)
Natural Mortality, M				1.0	0.367 (0.098)
Growth rate, k^1					1.0

¹ The parameter from the von Bertalanffy growth equation was used to represent the actual characteristics.

Table 8. Summary of the number of agreements between predicted and observed correlation coefficients among life history parameters within selected taxonomic groups.

Level of agreement	Number in agreement	Number possible	Percent in agreement
sign	46	46	100
5% probability level	40	46	87
1% probability level	31	46	67

predicted and observed correlations differs from the the number that would have occurred randomly. The number of agreements is significantly different than would have occurred randomly ($z = 4.86$, $P < 0.001$), when only correlations that were significant at the 5% level were used.

Response of r and K Selected Species to Harvesting

The interaction of life history characteristics will have a strong affect on the response of a species to fishing pressure. The Beverton and Holt yield per recruit equation estimates the yield that can be harvested from the growth of a cohort. The model assumes that fish growth is described by the von Bertalanffy growth curve and that mortality processes are exponential (Beverton and Holt 1957; Ricker 1975). The biological parameters in the model are: 1) M , the instantaneous rate of natural mortality, 2) W_{∞} , the mean asymptotic weight which corresponds to L_{∞} , 3) k , the von Bertalanffy growth coefficient, and 4) t_{∞} , the maximum age of a fish. From r and K selection, we can predict how these parameters will vary. Consider a situation with three hypothetical species: one species will be more r selected, another species will be more K selected and another will be intermediate between the first two. The biological parameters will vary as shown in Table 9. Beverton and Holt yield per recruit curves were calculated for a constant age at first recruitment ($t_r = 4.2$ yr) with a varying fishing mortality (Figure 7) and for a constant fishing mortality ($F = 0.25$) with a varying age at first recruitment (Figure 8).

The yield per recruit analysis points up that there are

Table 9. Biological parameters for use in yield per recruit analysis for three hypothetical r and K selected species.

Biological parameters	r selected species	Intermediate species	K Selected species
Natural mortality, M	0.30	0.20	0.10
Mean asymptotic weight, W_{∞}	641 g	1141 g	1641 g
von Bertalanffy growth coefficient, k	0.22	0.14	0.07
Maximum age, t_{∞}	13 yr	20 yr	35 yr

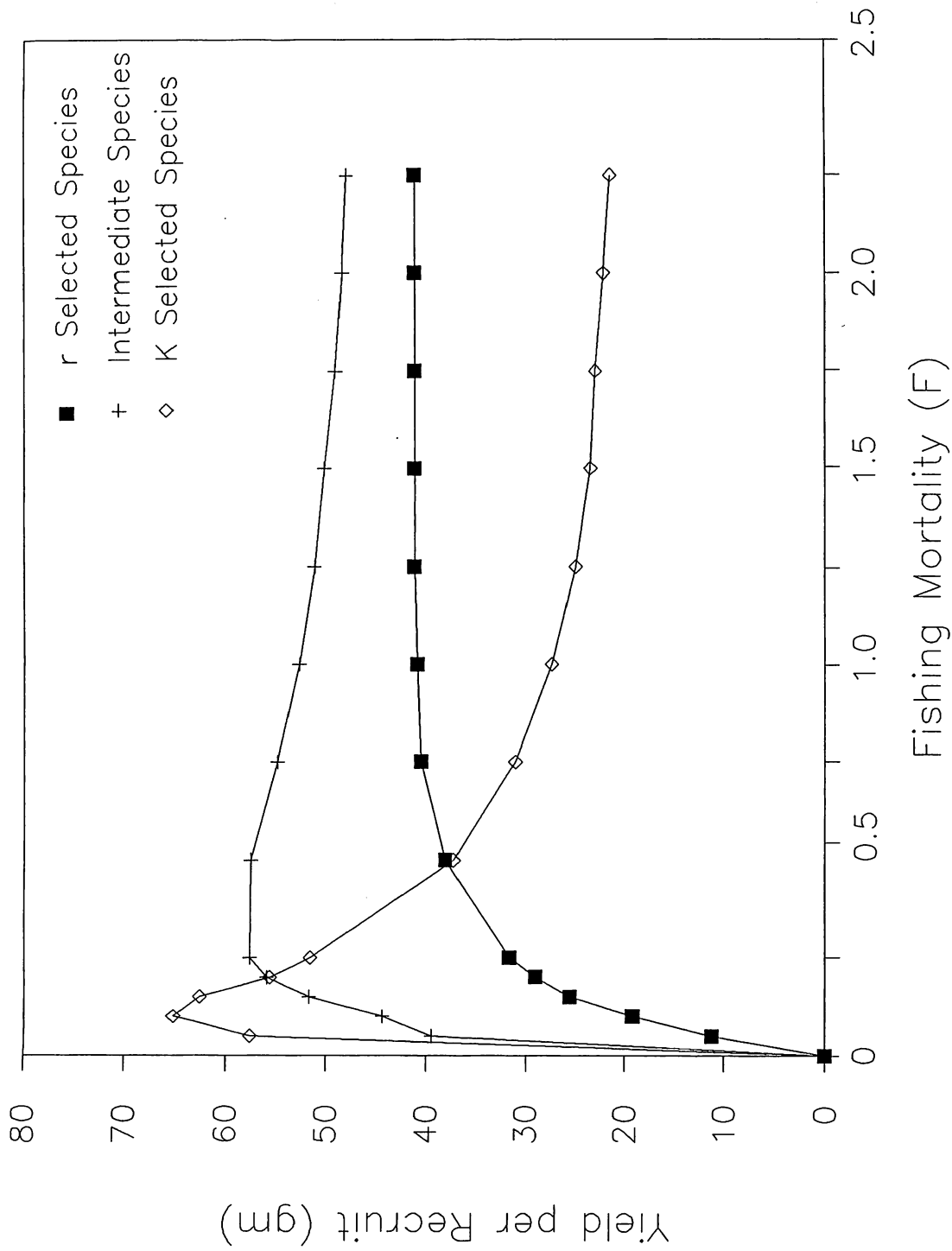


Figure 7. The effect of different levels of fishing mortality with constant age of recruitment (4.2 yr) on yield per recruit of three hypothetical fish species demonstrating the range of r and K selection.

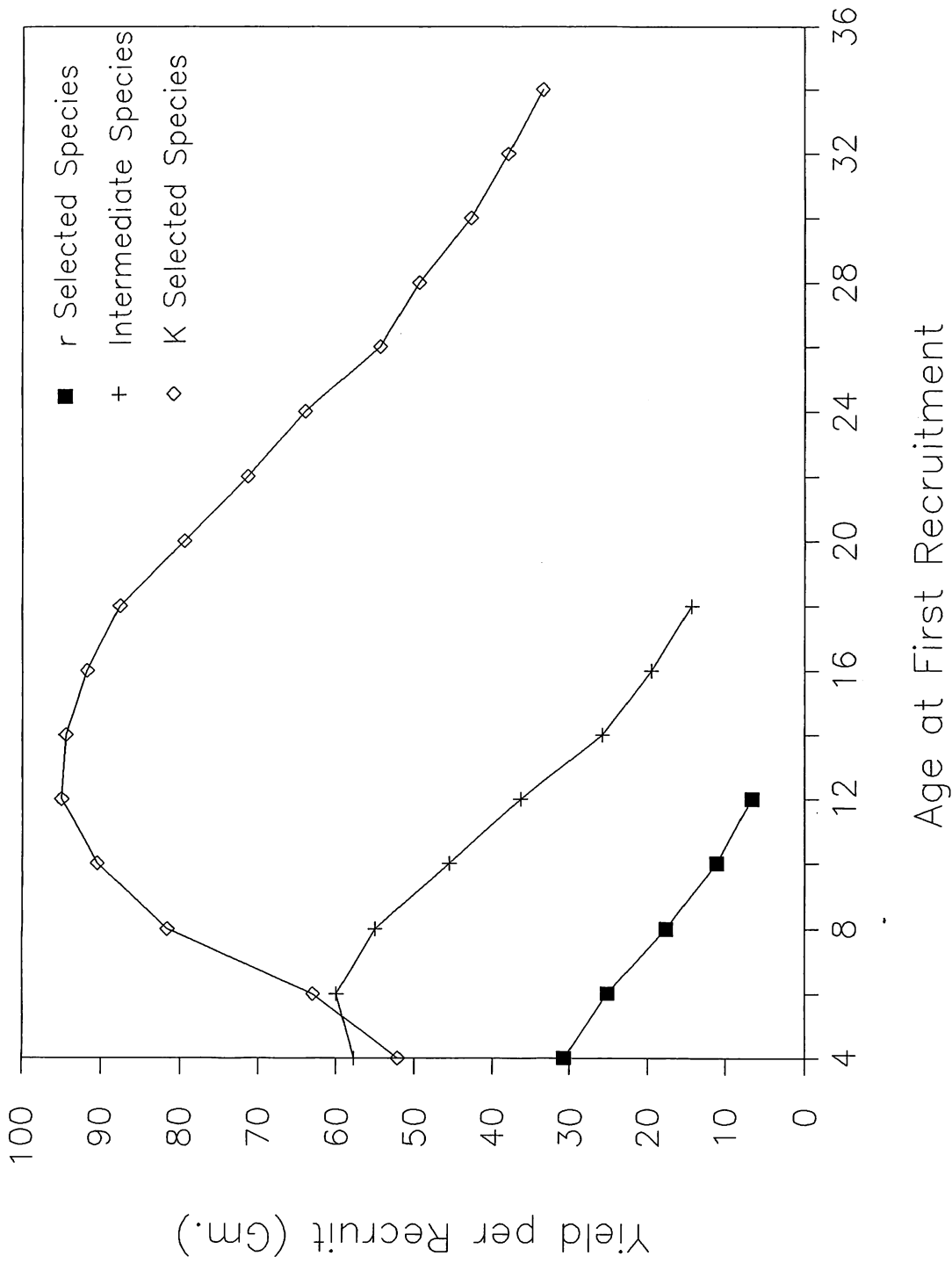


Figure 8. The effect of different mean ages of recruitment at a constant fishing mortality ($F = 0.25$) on yield per recruit of three hypothetical fish species demonstrating the range of r and K selection.

specific differences in fisheries based on r or K selected species. In fisheries based on K selected species, the maximum yield per recruit would occur at a lower level of fishing mortality and at a later age at first entry than in fisheries based on r selected species. The curves also indicate that K selected species would be much more sensitive to overfishing both in terms of fishing mortality and age at first entry.

The surplus production model of Schaefer combines reproductive and mortality functions into one parameter (Ricker 1975). The biological parameters in this model are B_{∞} , the maximum stock size (or carrying capacity in weight) and k , the instantaneous rate of increase of the stock at densities approaching zero. Again these parameters can be predicted for the three hypothetical species from r and K Selection (Table 10). In the surplus production model analysis (Figure 9), the r selected species have the highest productivity. As in the yield per recruit analysis, the maximum yield occurs at a lower fishing mortality for the K selected species than for the r selected species. The K selected species is reduced to levels lower than the maximum sustainable yield by overfishing much more rapidly than the r selected species.

Discussion

Life history parameters vary in consistent patterns. These patterns are explainable and predictable by the theoretical constructs of r and K selection. This is not a particularly new or unique idea in fisheries biology. Beverton and Holt (1959) investigated a positive

Table 10. Biological parameters for surplus production model analysis for three hypothetical r and K selected species.

Biological parameters	r selected species	Intermediate species	K Selected species
Maximum stock size, B_{∞}	1.54×10^8 g	2.04×10^8 g	2.54×10^8 g
Rate of increase, k	0.912	0.612	0.312

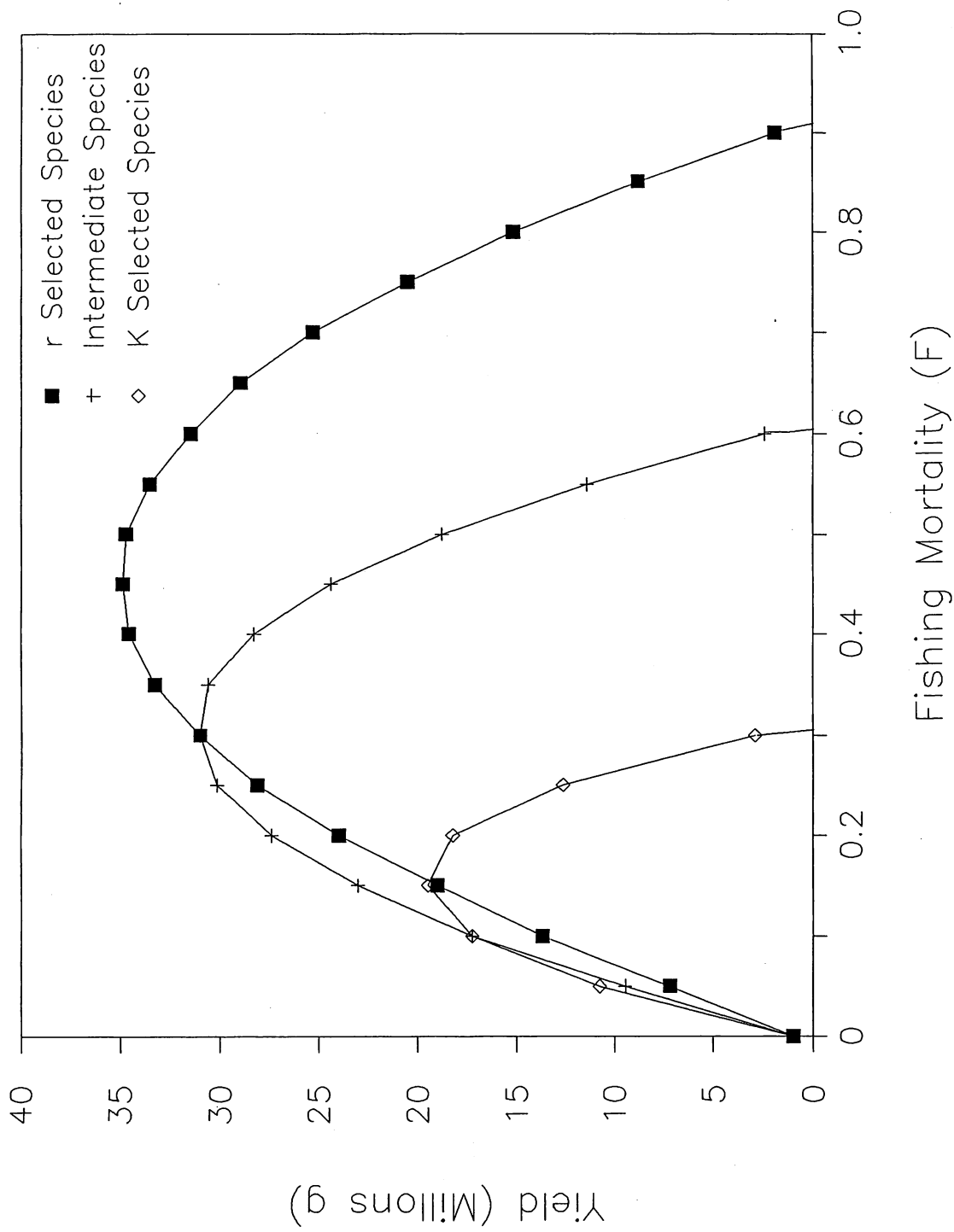


Figure 9. Maximum equilibrium yields (Millions g) from Schaefer surplus production curves as a function of fishing mortality for three hypothetical fish species demonstrating the range of r and K selection.

relationship between body size and life span and between mortality and growth rates. Cushing (1971) suggested that there is a negative relationship between degree of density dependent regulation and fecundity. Alverson and Carney (1975) have suggested a positive relationship between body size and the time when a cohort maximizes its biomass. In population ecology, similar relationships have been investigated for zooplankton (Allan 1976), plants (Gadgil and Solbrig 1972; MacNaughton 1975) and animals (Smith 1964; Bonner 1965). All these empirical observed trends described here, are consistent with r and K selection.

It is important to reemphasize here the comparative nature of r and K selection. The r and K continuum is a model and as such occurs only in an idealized sense. The idealized r selected species occurs in an ecological vacuum with no density effects and no competition. The idealized K selected species occurs in a completely saturated ecosystem where densities are high compared with carrying capacities and competition for resources is intense. The problem of applying this model to any real situation is not a trivial one. Species are simply subjected to a single set of selective pressures. Because of this, r and K concepts should only be applied in a comparative sense between groups of species that have some degree of functional similarity. No species is r selected or K selected in an absolute sense; it is only relatively more r selected or K selected than some other reference species. This theory will only have value in a situation where the population dynamics of one member of a species group are fairly well understood.

The results of the model analysis give several indications about the reaction to harvesting pressure of species which are more or less r or K selected. Fisheries based on more r selected species will be more productive. They can be fished at younger ages and at higher levels of fishing mortality. Given a minimum population size, these fisheries should also have a quicker recovery from overfishing. Species which are more r selected are likely to be strongly influenced by physical forces in the environment (Pianka 1974). Relationships of this type, e.g. between anchovies and upwelling, should be important considerations in management plans for these species.

Fisheries based on more K selected species will have a high maximum yield per recruit, but there will be fewer fish. Maximum equilibrium yield will occur at later ages of entry into the fishery and at lower levels of fishing mortality. These fisheries would be more susceptible to overfishing and stock depletion. Besides these species' sensitivity to overfishing, more K selected species are much more likely to have sophisticated life history mechanisms (Pianka 1974) which would have to be recognized in a management plan. These mechanisms might include parental care systems such as nesting or live births, mating systems or territoriality. The more K selected species are much more likely to have strong interspecific relationships, usually competitive ones. The relationship between competition and harvesting has been dealt with by Larkin (1963) and Tanner (1975). Additional density independent mortality (fishing mortality) increases the advantage for the

population with a higher population growth rate (i.e., more r selected). Therefore, even low levels of fishing pressure can destabilize a previously stable competitive pair and result in decline of the harvested species. Interestingly, the opposite result is also possible; harvesting pressure can stabilize a previously unstable species pair as Slobodkin (1962) found with experimental populations of hydra.

Fisheries based on more K selected species, in contrast to the boom and bust nature of r selected fisheries, will be characterized by relatively stable population sizes and therefore catch levels. Given some initial measure of year class strength, possibly through larval or prerecruitment surveys, the prediction of future catches from that fishery could be made with a fair degree of accuracy. However, once fisheries based on these species become overfished, it would require a long period for the stock to rebuild to levels which can support economical profitable fisheries. An extremely K selected species would only be suitable for trophy fisheries.

Fisheries based on r and k selected species have been discussed in a comparative sense, but predation (in this case of a fishery, human predation) will also have effects on an individual species. The gene pool of any species is going to contain within it some range of variation of both r and K selected traits. The effects of increasing fishing mortality, which is assumed to be density independent (Cushing 1975), on life history characteristics has been theoretically analyzed by Roughgarden (1971). The general effect is an increase in selective advantage for the r selected proportions of the gene

pool. This would mean an increase in growth rates, reduced age at first maturity and greater fecundity at age. These trends will be more conspicuous in species that are relatively more K selected. Species that are more strongly r selected are likely to have less range of variation in this direction. One example of these effects of predation pressure is a comparison of lake trout, Salvelinus namaycush, populations under heavy predation pressure from the freshwater harbor seal, Phoca vitulina, to populations in nearby lakes without seals (Powers and Gregoire 1978). The lake trout populations which were preyed upon by seals had faster growth rates, small maximum body size, reduced maximum age, lower age at sexual maturity and greater individual fecundity compared with populations in lakes without seals. Growth and maturation rates of certain seal species have also increased where populations have been reduced by fisheries (Sergeant 1973). These affects can be attributed to changes in selection pressure resulting from sustained harvesting.

In summary, r and K selection seems to have been an important evolutionary trend on marine fish populations. The basic hypothesis are confirmed by the data presented here. The result of patterns in population parameters which arise from r and K selection is that different management strategies would be appropriate. The value of this approach is likely to be in initial stages of development of a fishery. As a fishery becomes more developed and more specific information becomes available, a more refined management strategy would become possible.

Appendix I: Literature Citations for Population Parameters by
Species

Herring and Anchovies, Families Clupeidae and Engraulidae

Clupea harengus - Lea 1919; Sund 1943a,b; Jensen 1947;

Fridriksson 1950,1951-61; Alander 1950; Tibbo 1956,1957a,b;

Hannerz 195; Gilis 1957-1961; Smith 1957; Day 1957; Cushing 1959;

Nielsen 1960; Burd 1962; Parrish and Craig 1963; Postuma 1963;

Bowers 1963.

C. pallasii - Hanamura 1953; Tester 1955; Ricker 1958; Tanaka

1960; Ayushin 1963; Motoda and Hirano 1963.

Sprattus sprattus - Robertson 1938; Molander 1943; Faure 1950;

Elwertowski 1957-1960.

Sardinops caerulea - Silliman 1943; Phillips 1948; Mosher and

Eckles 1954; Clark and Marr 1955; Murphy 1966; Culley 1971.

S. melanosticata - Tanaka 1960; Tokai Regional Fisheries Research
Laboratory 1960.

S. neopilchardus - Blackburn 1950.

S. ocellata - Davies 1958; DeJager 1960; Culley 1971.

Sardina pilchardus - Hodgson and Richardson 1949; Bough

1952; Hodgson 1957; Larraneta 1960; Cushing 1961; Culley 1971.

Sardinella aurita - Postel 1955; Rossignol 1955; Richardson et
al. 1960; Ben-Tuvia 1960; Beverton 1963.

S. longiceps - Nair 1960.

Engraulis encrasicolus - Fage 1920; Furnestin 1945.

E. japonicus - Hayashi and Kondo 1957; Watanbe 1958; Tanaka 1960;
Hayashi 1961.

E. mordax mordax - Clark and Phillips 1952; Miller et al. 1955;
Miller and Wolf 1958; Culley 1971.

Cetengraulis mysticetus - Barrett and Howard 1961.

Salmons, Family Salmonidae

Coregonus clupeaformis - Hart 1931; Hile and Deason 1934; Kennedy
1943, 1953; Ricker 1949.

Cristivomer namaycush - Kennedy 1954.

Leucichthys artedii - Hile 1936.

L. kiyi - Deason and Hile 1947.

Onchorhynchus kisutch - Shapovalov and Taft 1954; Drucker 1972.

O. nerka - Foerster 1968; Van Cleve and Bevan 1973.

Cods, Family Gadidae

Borogadus saida - Beverton and Holt 1959.

Gadus callarias - Beverton and Holt 1957; Taylor 1958.

G. macrocephalus - Ketchen 1964.

G. minutus - Menon 1950.

G. morhua - Fleming 1960; Pinhorn 1969; Clayden 1972.

G. virens - Beverton and Holt 1959.

Melanogrammus aeglefinus - Raitt 1939; Beverton and Holt 1959.

Rockfishes, Family Scorpaenidae, Genus Sebastes

Sebastes crameri - Phillips 1964.

S. diploproa - Phillips 1964.

S. entomelas - Phillips 1964.
S. flavidus - Phillips 1964.
S. goodei - Phillips 1964.
S. jordani - Phillips 1964.
S. miniatus - Phillips 1964.
S. paucispinis - Phillips 1964.
S. pinniger - Phillips 1964.
S. saxicola - Phillips 1964.

Flatfishes, Order Pleuronectiformes

Citharichthys sordidus - Arora 1951.
Eopsetta jordani - Ketchen and Forrester 1966.
Hippoglossus platessoides - Powles 1965,1969; MacKinnon 1973.
H. vulgaris - Beverton and Holt 1959.
Isopsetta isolepis - Hart 1948.
Pleuronectes platessa - Beverton and Holt 1959.
Pseudopleuronectes americanus - Dickie and McCracken 1955.
Solea vulgaris - Beverton and Holt 1957.

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