# A MULTISPECIES ANALYSIS OF THE COMMERCIAL DEEP-SEA HANDLINE FISHERY IN HAWAII 

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#### Abstract

In the Hawaiian Islands 13 species of bottom fish are commonly harvested in the commercial deepsea handline fishery. These are all high-level carnivores, including snappers, jacks, and a species of grouper, which are sought in water depths ranging from 60 to 350 m . Cluster analyses performed on the Hawaii Division of Fish and Game commercial catch report data suggest the existence of three bottom fish species groups which apparently segregate on the basis of depth distribution. These groups seem to be stable through time and similar among differing geographic localities. Two measures of fishing effort, catch-records and fisherman-days, were compared to determine which is more suitable for use in stock-production analyses. Fisherman-days was selected because, among other reasons, it repeatedly demonstrates a stronger negative correlation with catch per unit effort. Application of the Schaefer stock-production model to this multispecies fishery on a species-byspecies basis provides an inadequate description of productivity. When catch statistics are aggregated according to the three cluster analysis species groups the results are much improved. In this regard consistently significant results and production estimates were obtained from the Maui-Lanai-Kahoolawe-Molokai bank, a region which presently accounts for about half of the total Hawaii catch. No significant interaction among the cluster groups was detected. When all 13 bottom fish species are analyzed together, the results are in agreement with the preceding analysis. Examining the aggregation process suggests that the model based on the intermediate level of aggregation (cluster groups) explains slightly more of the variation in total catch than does the model which treats all 13 species together. We estimate the annual maximum sustainable yield of the commercial deep-sea handline fishery around the Maui-Lanai-Kahoolawe-Molokai bank to be 106 metric tons or about $272 \mathrm{~kg} / \mathrm{nmi}$ of 100 fathom isobath. Because recreational catch is unaccounted for these figures are considered lower bounds for the gross production obtainable from this type of fishery although currently the commercial fishery is operating close to this maximum-sustainable-yield level.


Effective management programs for tropical fisheries are difficult to achieve (Pauly 1979). Often attempts at managing these fisheries are based on the application of inappropriate models to sparse data. Both deficiencies are due in part to the multiplicity of fish species inhabiting tropical environments. This great diversity (Sale 1977; Talbot et al. 1979) makes it difficult to compile adequate data for all species of interest. The Hawaiian Islands, which straddle the Tropic of Cancer, possess a relatively impoverished tropical ichthyofauna, yet between 600 and 700 species are known from this region (Gosline and Brock 1960). Coupled with high diversity,

[^0]many tropical countries lack a refined statistical system for the acquisition and storage of fisheries data. In concert these two limitations impose severe restrictions on the quantity and quality of data which are currently available for the analysis and management of tropical fisheries (Pope 1979). Furthermore, classical fisheries models thus far developed have been directed toward the management of temperate and boreal stocks (Food and Agriculture Organization of the United Nations (FAO) 1978). These models usually treat species as independent management units. It has become apparent that such an approach is often inadequate when extrapolated to the tropics where community dynamics become increasingly important (Pauly 1979).

The multispecies approach to managing fisheries exploitation in complex ecosystems has only recently acquired a substantive base in the literature. Early work by Larkin $(1963,1966)$
evaluated the consequences of Lotka-Volterra competition and predator-prey systems on optimum exploitation strategies. Paulik et al. (1967) examined the problem of maximizing the yield from a fishery composed of mixed stocks, each with a unique spawner-recruit curve. A large body of descriptive work has documented the successional nature of changing catch composition which is often characteristic of increasing exploitation in a multispecies fishery (e.g., Regier 1973). Several recent multispecies investigations present highly sophisticated ecosystem models that require numerical solution and/or dynamic simulation, as well as numerous parameter estimates (Parrish 1975; Andersen and Ursin 1977; Laevastu and Favorite $1978^{3}$ ).

An alternative to this latter approach simply treats multispecies fisheries as though they behave as would a single species stock and evaluates production by application of the total biomass Schaefer model (TBSM) (Pope 1979). Brown et al. (1976) estimated total finfish production in the northwest Atlantic in this manner, as did Brander (1977) for demersal fish and shellfish in the Irish Sea. A review of this approach shows that "these overall Schaefer models generally seem to fit the data rather better than the fits experienced with their component stocks" (FAO 1978). Among the possible reasons for this are 1) the TBSM really presents a more realistic representation of multispecies fisheries than does summing the yields of individual stocks, 2) the better fit results from some type of averaging process, 3) artifacts in the method of fitting and/or shifts in preference between species within a fishery may result in a better fit when total biomass is evaluated (FAO 1978; Pauly 1979; Pope 1979). Several authors have issued the caveat that a thorough understanding of trophic relations is fundamental to managing any multispecies fishery and that such considerations may easily invalidate the application of the TBSM (May et al. 1979; Pauly 1979).

This paper estimates the productivity of deepdwelling bottom fish stocks around the main islands of the Hawaiian Archipelago using stockproduction methods. The fishery for these stocks is conducted in offshore waters ranging in depth from 60 to 350 m where a variety of species, prin-

[^1]cipally snappers of the Family Lutjanidae, abound. In addition to providing preliminary productivity estimates for this fishery, an examination of the performance of the TBSM at various levels of species aggregation is undertaken. This latter analysis provides a quasiquantitative means of evaluating the applicability of the TBSM to the Hawaiian offshore handline fishery.

## SOURCES OF DATA AND DESCRIPTION OF THE FISHERY

In the State of Hawaii, all fishermen who sell a portion of their catch must be licensed as commercial fishermen by the Hawaii Division of Fish and Game (HDFG). There is no licensing requirement for recreational fishing. New commercial licenses are issued every fiscal year and once licensed, fishermen are required to submit a monthly catch report whether or not they have fished. These monthly catch reports require from each fisherman entries on the days and areas in which he fished, the types of fishing gear used, the number of individuals and pounds of the different species landed, and the dollar value of the catch. Incomplete reporting is thought to be common and raises the question of bias in the data (Ralston $1979^{4}$ ). Perhaps more serious is the omission of any direct measure of fishing effort or fishing power in the information concerning bottom fish obtained from these reports.
Monthly catch reports are coded, keypunched, and stored on magnetic tape for future use by HDFG. These data are the basis of this study and currently span the $20-\mathrm{yr}$ period 1959 to 1978 inclusive, comprising some 600,000 records. While the date are voluminous, the extent of nonreporting by recreational fishermen and of incomplete or underreporting by commercial fishermen is unknown.
The complete HDFG data account for all types of commercial fishing in the State of Hawaii; therefore, only those catch records which list deep-sea handline fishing gear were used in this study. This reduced the data to one-fourth its original size and defined the scope of the fishery. Although the name suggests otherwise, the fishing gear is primarily hydraulic or electric

[^2]although some manual equipment remains in use.

The fishery mainly exploits 13 categories of fish species (Table 1). Confusion concerning the taxonomy of species in the family Carangidae prohibits a more detailed classification of these forms although Pseudocaranx dentex and Caranx ignobilis probably account for the majority of ulua landed in Hawaii. While $P$. dentex is abundant in the Northwestern Hawaiian Islands, it is apparently uncommon around the main high islands (Uchida ${ }^{5}$ ). Further confusion is apt to result from the findings of Anderson (1981), who recently revised the genus Etelis and changed the names of both Hawaiian species. In addition, two hogfish species are frequently taken, Bodianus bilunulatus and B. vulpinus, although the former species seems to inhabit somewhat shallower depths than the latter. Of those species listed, most are caught almost exclusively with deep-sea handline gear. The exceptions are ta'ape, ulua, and a'awa which are commonly taken by several other methods (e.g., inshore handline, purse seine, gill net, etc.) (Ralston footnote 4). Catches of these species reported here include only those portions taken in the offshore handline fishery.
In descending order the dominant species in the fishery by weight are the opakapaka, ulua, uku, onaga, hapu'upu'u, and kahala (Ralston

[^3]Table 1.-Principal species of fish landed in the Hawaiian offshore handline fishery.

| Family | Species | Common name | Average weight (kg) |
| :---: | :---: | :---: | :---: |
| Lutjanidae | Aphareus rutilans | Lehi | 3-8 |
|  | Aprion virescens | Uku | 2-8 |
|  | Etelis coruscans | Onaga | 2-8 |
|  | E. carbunculus | Ehu | 0.5-2 |
|  | Lutjanus kasmira | Ta'ape | 0.5 |
|  | Pristipomoides filamentosus | Opakapaka | 1-6 |
|  | P. sieboldii | Kalekale | 0.5 |
|  | P. zonatus | Gindai | 0.5-2 |
| Carangidae | Caranx and Carangoides spp. | Ulua | 1-10 |
|  | Seriola dumerili | Kahala | 3-1.0 |
| Serranidae | Epinephelus quernus | Hapu'upu'u | 3-10 |
| Labridae | Bodianus spp. | A'awa | 1-3 |
| Scorpaenidae | Pontinus macrocephala | Nohu | 1-2 |

footnote 4). These species taken together accounted for $86 \%$ of the total catch by weight in 1978, nearly all of which was marketed in Hawaii as fresh fish. Total landings from the fishery have remained relatively constant from 1959 to 1978, showing a slight increase in recent years, although higher catches were briefly reported during the late 1940 's and early 1950 's (Fig. 1) (Ralston footnote 4). Most of these species are highly prized and in recent years have averaged close to $\$ 5.00 / \mathrm{kg}$ ex-vessel.

In the past about $85 \%$ of the catch of deep dwelling bottom fish has been made around the main Hawaiian Islands in contrast to the uninhabited Northwestern Hawaiian Islands (Grigg and Pfund 1980). Catches from the latter area have increased remarkably in the last 2 yr , as larger, more seaworthy vessels have entered the fishery. Nonetheless, the lack of sufficient data


Figure 1.-Annual landings and total annual effort for the commercial deep-sea handline fishery in the main high islands of the Hawaiian Archipelago.
from this region prevents its analysis; the results presented here pertain only to the eight main islands of the archipelago (Hawaii, Maui, Kahoolawe, Lanai, Molokai, Oahu, Kauai, and Niihau, including Kaula Rock). Within this region fishing is conducted on offshore banks and pinnacles, primarily in the vicinity of the 100 -fathom isobath. In the Hawaiian Islands the sea bottom typically extends away from shore at a depth of 30 fathoms for some distance and then falls abruptly to very great depths over a relatively short horizontal span (Brock and Chamberlain 1968). Most fishing occurs in this steep dropoff zone. Hence it is possible to crudely estimate the relative amount of total bottom fish habitat around a fishing bank by determining the length of the 100 -fathom isobath surrounding it (Table 2). The maximum depth between the islands of Maui, Lanai, Kahoolawe, and Molokai (MLKM) is <100 fathoms; therefore, they were pooled and treated as a single bank (Fig. 2). All bottom fish taken from a bank were considered one stock because movements of juveniles and adults across deep water from one bank to the next are highly improbable whereas lateral movements around the perimeter of the 100 -fathom isobath of a bank cannot be discounted. The Islands of Oahu and Hawaii are separated by deep water from all other islands and banks, hence, by definition, they harbor distinct stocks. Kauai, Niihau, and Kaula Rock

Table 2.-A list of the four banks which harbor separately defined stocks. The length of the 100 -fathom isobath around a bank roughly measures the extent of its bottom fish habitat.

| Bank | Percent contribution <br> to total landings | Approximate length of <br> 100-fathom isobath (nmi) |
| :--- | :---: | :---: |
| Hawaii | 21 | 290 |
| MLKM | 56 | 390 |
| Oahu | 12 | 150 |
| KNK | 11 | 195 |
| 'Maui-Lanai-Kahoolawe-Molokai. |  |  |
| 'Kauai, Niihau, and Kaula Rock. |  |  |

(KNK), although separated across short distances by deep water, were analyzed together because they present a similar fishing profile and they are closely situated to one another. Thus, based on this classification four distinct stocks were analyzed independently. The extent of larval dispersal between these stocks is unknown at present but is currently under study (Shaklee ${ }^{6}$ ). A more detailed description of this fishery may be found in Ralston (footnote 4) or in Hawaii Department of Land and Natural Resources (1979).

## FISHING EFFORT

The ultimate goal of any stock-production analysis is to relate the impact of variable fishing pressure on stock abundance. Fishing pressure
${ }^{6}$ J. G. Shaklee, Hawaii Institute of Marine Biology, University of Hawaii, Kaneohe, HI 96744, pers. commun. 1979.


Figure 2.-Map of the eight main Hawaiian Islands and Kaula Rock with the 100 -fathom isobath included.
is most conveniently formulated as instantaneous fishing mortality ( $F$ ), measured over some arbitrary interval of time, usually 1 yr (Ricker 1975). Frequently it is not possible to measure $F$ directly, however, and so a proportionate measure of $F$ is selected, i.e., fishing effort or $f$. The ideal choice of units for fishing effort results in a linear correspondence between $F$ and $f$, a zero intercept, and minimal residual variance (Rothschild 1977). Because $F$ is frequently unknown, it is often difficult to ascertain whether these criteria are met and yet the selection of an appropriate measure of fishing effort is most critical to meeting the assumptions of a stock-production analysis. Ample consideration should be given to these factors before the data are collected.

No attempt has been made in the HDFG data to record either the fishing effort or the fishing power of individual fishermen. A suitable measure of fishing mortality in this fishery would be the cumulative number of hook-hours or line-hours of fishing. While such figures are currently unavailable, it has been possible to determine the total number of fishing records filed in a year which report the catch of a particular species. This statistic, the number of daily reports by fishermen who have caught any one particular species, was frequently computed and is termed catch-records. Figure 1 presents, in addition to the catch, the total number of deepsea handline catch-records filed from 1959 to 1978 concerning all 13 species of bottom fish. This measure of fishing effort does not always correspond to the number of fisherman-days because one operator may catch several species during a single day of fishing. In this instance the reporting of each particular species comprises one catch-record. Thus, when aggregated species groups are considered, the number of fish-erman-days will always be fewer than the total number of catch-records. When species are considered independently of one another the two figures are equal (catch-records = fisherman-days).

Interpreting the meaning of a fisherman-day as a unit of fishing effort in this fishery is difficult. It was tabulated by following the daily reports of individual fishermen, identified by their commercial fishing license numbers. All commercial fishermen in Hawaii, whether captain or crew, must have a license. It is likely that many catch reports are filed only by boat captains who document the landings of an entire fishing vessel, which may have a variable
number of crew members. Thus a fishermanday, as defined here, may reasonably be thought of as a vessel-day. However, because this unit of effort is defined and specified on the basis of commercial fishing licenses, in the interests of exactitude, we have chosen to use the term fisherman-day.

## RESULTS

## Clustering

The usual method of aggregating catch data would be to pool all 13 deep-sea handline species into a single group and to analyze the total with the TBSM. An alternative is to employ a multivariate statistical procedure to assess the degree of colinearity among species and to define species groups based on the strength of interspecies associations in the catch (Pope 1979). Such an approach would identify those bottom fish which tended to appear with one another in the catch to the exclusion of others and would measure the extent of correlation of fishing mortality among species. Pope (1979) has termed this "technological interaction" and has discussed its importance in multispecies fisheries. Separate application of the TBSM to each species group formed by clustering would constitute an analysis performed at an intermediate level of species aggregation. Conceptually this is desirable because in the Hawaiian offshore handline fishery different species are known to exhibit stratification by depth (Strasburg et al. 1968).

Cluster analyses were performed with a computer routine (Dixon 1977, program P1M) where the 13 species of bottom fish comprised the variables to be clustered and the catch from a single day's fishing formed one case. Associations were computed on the basis of the landed weight of each species. The average linkage between groups defined the criterion for amalgamating clusters and correlation coefficients were used as measures of similarity.

Separate analyses were performed for each of the four designated bank (Table 2) areas to assess whether obvious differences exist among banks with regard to interspecies associations. Similarly, separate analyses were conducted for the years 1959, 1965, 1971, and 1977 to see whether temporal variation in species grouping is an important factor to consider.

No striking differences or patterns emerged from these various comparisons. The intrinsic
variation apparent between clusters obtained from the same bank in 3 adjacent years (Hawaii in 1976, 1977, and 1978) was as great as the variation in clustering found between different banks and through longer periods of time. While there were a few suggestions of differences in the species composition of groups among the four banks, these were relatively minor and were ignored. Only one fairly consistent pattern of grouping was repeatedly exhibited across banks and through time, and this was confirmed by a single clustering of all the data pooled together. This pattern shows that the bottom fish fishery is loosely composed of three species groups which are apparently segregated on the basis of the depth range of member species (Table 3) (for depth distributions see Gosline and Brock 1960; Brock and Chamberlain 1968; Strasburg et al. 1968). These groups represent species assemblages which are for the most part independent of time and/or geographic location.

The delimitation of these three species groups is somewhat arbitrary and should not be viewed as the only way in which an intermediate level of species aggregation of the catch could be achieved. Nevertheless this grouping structure is reasonable and its use enhances the biological realism of the multispecies model by identifying and classifying those species which seem to share the greatest correlation in fishing mortalities. In addition the grouping structure allows an assessment of the effect aggregation has on the fit of data to a Schaefer stock-production analysis. A brief discussion of each of these groups is appropriate.

The appearance of ulua, ta'ape, and a'awa in the shallowest group (Group I) is consistent with the observation that these three species are frequently harvested with other types of fishing gear. Members of this group are often seen by scuba divers who venture below 30 m , although the vertical distribution of these species in the deep-sea handline fishery is centered around the 60 m terrace which circles much of the Hawaiian Islands (Brock and Chamberlain 1968). Because the name ulua refers to several different carangid species, one of which ( $P$. dentex) is most often taken with members of Group II in deeper water, it is evident that some inaccuracies in the classification exist. This particular defect is not so much a result of the clustering process as it is a result of faulty data. Kahala, on the other hand, range widely (Gosline and Brock 1960) and are known from throughout the depth ranges of both

Table 3.-Bottom fish species groupings defined by cluster analysis.

| Group | Species | Approximate depth <br> range $(\mathrm{m})$ |
| :---: | :--- | :---: |
| I | Ulua, uku, ta'ape, a'awa | $30-140$ |
| II | Opakapaka, hapu'upu'u, kahala, | gindai, lehi, nohu |
| III | Onaga, ehu, kalekale | $80-240$ |

Groups I and II and occur even shallower. Its position in Group II may simply reflect the relatively greater fishing pressure exerted in the $100-200 \mathrm{~m}$ depth range where other members of Group II, such as the opakapaka and hapu'upu'u, are centered. The deepest group (Group III) is particularly well defined and is composed of three lutjanid species, two of which are deepwater eteline red snappers.

## Fishing Effort

An attempt was made to evaluate the two measures of fishing effort, catch-records and fisher-man-days, on the basis of their correlation with catch per unit of effort (CPUE). The Schaefer model predicts that plots of CPUE against effort should demonstrate a linear relationship with a negative slope if the production of the stock is described by the logistic growth curve (Ricker 1975). Such a prediction generates a one-tailed test of the hypothesis that $\rho \geq 0$ against the alternative hypothesis that $\rho<0$ where $\rho$ is the population correlation coefficient between CPUE and $f$. Even though a negative correlation between CPUE and effort is expected in a situation where catch and effort are completely unrelated random variables, the degree of spurious correlation due to this effect will be small if the main cause of variation in CPUE is varying stock abundance (Gulland 1974).

Correlations were computed between these two variables, using both measures of fishing effort for each species group-bank combination ( $3 \times 4=12$ ). Additional correlations were computed for the total aggregated catch from each of the four banks $(1 \times 4=4)$, resulting in 16 comparisons of the two measures of effort (Table 4). Comparisons which might be based on treating species as independent stocks are inappropriate here because the two measures of effort become equal in this limiting case. One means of evaluating the effectiveness of these two measures is to compare the signs of the correlation coefficients ( $r$ ) and the magnitudes of the coefficients of determination $\left(r^{2}\right)$ for each. It

Table 4.-Comparisons of correlations of CPUE and fishing effort (f) for two different measures of $f$. The total aggregate incorporates all 13 species.

| Group | Bank' | Unit of fishing effort |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | Catch-records |  | Fisherman-days |  |
|  |  | $r$ | $r^{2}$ | $r$ | $r^{2}$ |
| 1 | Hawaii | -0.095 | 0.01 | -0.128 | 0.02 |
|  | MLKM | -0.358 | 0.13 | ${ }^{2}-0.503$ | 0.25 |
|  | Oahu | -0.153 | 0.02 | -0.259 | 0.07 |
|  | KNK | -0.180 | 0.03 | -0.111 | 0.01 |
| 11 | Hawaii | -0.111 | 0.01 | -0.120 | 0.01 |
|  | MLKM | $-0.379$ | 0.14 | ${ }^{2}-0.769$ | 0.59 |
|  | Oahu | +0.285 | 0.08 | +0.293 | 0.09 |
|  | KNK | +0.481 | 0.23 | +0.237 | 0.06 |
| III | Hawaii | -0.187 | 0.03 | -0.015 | 0.00 |
|  | MLKM | -0.240 | 0.06 | ${ }^{2}-0.502$ | 0.25 |
|  | Oahu | -0.362 | 0.13 | ${ }^{2}-0.390$ | 0.15 |
|  | KNK | -0.308 | 0.09 | ${ }^{2}-0.395$ | 0.16 |
|  | Total aggregate |  |  |  |  |
|  | Hawaii | -0.150 | 0.02 | -0.334 | 0.11 |
|  | MLKM | ${ }^{2}-0.463$ | 0.21 | ${ }^{2}-0.878$ | 0.77 |
|  | Oahu | ${ }^{2}-0.465$ | 0.22 | ${ }^{2}-0.521$ | 0.27 |
|  | KNK | +0.395 | 0.16 | -0.165 | 0.03 |
| ${ }^{1}$ MLKM $=$ Maui-Lanai-Kahoolawe-Molokai KNK = Kauai, Niihau, and Kaula Rock. ${ }^{2}$ Significant at $P=0.05$ level, one-tailed test, of $=18$. |  |  |  |  |  |

is apparent that in 13 of the 16 possible comparisons, fisherman-days showed a stronger negative correlation with CPUE than did catch-records. Based on these results we conclude that fisherman-days predicts the behavior of CPUE more precisely than catch-records. Use of this measure also eliminates repeated counting of effort statistics when more than one species in a group is caught on a particular day and has greater intuitive appeal as well. For these reasons we conclude that fisherman-days is the best measure of fishing effort available at present. It is worth noting that these two different measures of effort are approximately linear in their relationship to one another, implying that the superiority of fisherman-days over catch-records as a measure of effort is probably due to a smaller residual variance of instantaneous fishing mortality ( $F$ ) on the former statistic than on the latter.

## Stock Production Analyses

In this section the Schaefer model is applied to the deep-sea handline data in which the catch is aggregated at three different levels. At the first level a single-species Schaefer model is fitted to each species separately. Next, the TBSM is fitted to each of the three species groups delimited by the cluster analysis. In the final section the total aggregated catch of all 13 species taken together is analyzed with the TBSM. Fisherman-days was used as the measure of fishing effort throughout, but equilibrium approximation
(Gulland 1972) was not attempted because no information was available concerning the longevity of these species and a previous application of this method to the data had shown little improvement in the results (Ralston footnote 4).

When each species is treated independently there are 52 separate analyses ( 4 banks with 13 species each). In only two of these regressions of CPUE on $f$ is the null hypothesis $\beta \geq 0$, where $\beta$ is the slope of the regression, rejected in favor of the alternative hypothesis $\beta<0$. Both involved the MLKM bank where opakapaka ( $t=-2.91, \mathrm{df}=$ 18 ) and uku ( $t=-1.82, \mathrm{df}=18$ ) demonstrated significant inverse regressions in which respec tively, $32 \%$ and $16 \%$ of the total variation in CPUE were explained. The significance of these two regressions can easily be attributed to the Type I error and consequently nothing can be concluded from these results concerning the productivity of these fishes.
The fit of the TBSM to the data is much improved when the three species groups are considered. The model was applied to the HDFG data 12 times; once for each species group and bank combination. Significant results ( $P=0.05$, one-tailed test) were obtained in 5 of the 12 applications of the model (Table 5). The three analyses from the MLKM bank were significant in every case and those for Group III were significant in three out of the four regressions tested. The observation that the results from the remaining banks and species groups are not significant is not so disturbing because $56 \%$ of all bottom fish landings are harvested from the MLKM bank (Table 2). An estimate of the maximum sustainable yield (MSY) and optimum effort was then computed for each of the five significant combinations, as well as a standardized measure of productivity, calculated as the sustainable yield of bottom fish per nautical mile of 100 -fathom isobath. Assuming logistic growth of the stocks the catchability coefficient was estimated using the computer program PRODFIT (Fox 1975). The $t$ value in the table refers to the test of the null hypothesis that the slope of a regression is zero or positive.
Pope (1979) has proposed an interactive model to describe multispecies fisheries in which total yield is depicted as the sum of the yields of individual species with additional terms to account for community interactions. In the simple two-species case the equation describing surplus production $(Y)$ is:

Table 5.-Significant applications of the total biomass Schaefer model to the Hawaii Division of Fish and Game data set where species have been aggregated according to cluster analysis species groupings.

| Bank ${ }^{1}$ | Species group | $\begin{gathered} \mathrm{MSY}^{2} \\ (\mathrm{~kg} / \mathrm{yr}) \end{gathered}$ | Optimum effort (fisherman-days) | MSY/nmi 100-fathom isobath | Catchability coefficient | ivalue $(\mathrm{df}=18)$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| MLKM | 1 | 23,000 | 480 | 60 | 0.00180 | $-2.47$ |
|  | 11 | 48,800 | 662 | 125 | 0.00062 | -5.11 |
|  | III | 31,900 | 396 | 82 | 0.00120 | -2.46 |
| Oahu | 111 | 1,900 | 119 | 12 | 0.00280 | -1.74 |
| KNK | III | 4.800 | 84 | 25 | 0.00600 | -1.77 |

TMLKM $=$ Maui-Lanai-Kahoolawe-Molokai
KNK
${ }^{\text {KNK }}=$ Kauai, Niihau, and Kaula Rock
${ }^{2} \mathrm{MSY}=$ maximum sustainable yield.

$$
\begin{align*}
Y= & a_{1} N_{1}+a_{2} N_{2}-b_{1} N_{1}^{2}-b_{2} N_{2}^{2} \\
& +\left(c_{1}+c_{2}\right) N_{1} N_{2} \tag{1}
\end{align*}
$$

where $N_{1}$ and $N_{2}$ refer to the population sizes of species one and two and $a_{1}, a_{2}, b_{1}, b_{2}, c_{1}$, and $c_{2}$ are model parameters (Pope 1979). This model is the sum of two single-species surplus production models with the additional term $\left(c_{1}+c_{2}\right) N_{1} N_{2}$ to account for the interaction between the two species. Depending upon the signs of $c_{1}$ and $c_{2}$ the equation models predation, competition, or mutualism. More importantly, the sum of these two parameters determines the impact of the interaction on the sustainable yield of the system.

The question of whether significant interaction occurs among the cluster-analysis species groups was examined by considering the MLKM bank alone. The regressions of all three cluster groups were highly significant from this region and further treatment of these data is therefore considered appropriate.

In the three-species version of Equation (1) there are three terms involving the sum of $c$ parameters. In this analysis a species group (I, II, or III) is treated as though it were a single species and the $a$ and $b$ parameters necessary to evaluate the equation were taken from the independently calculated regressions of Table 5. A nonlinear regression routine (SAS Institute 1979, program NLIN) was employed to estimate the sums of the various $c$ parameters for the MLKM bank (Table 6). It is apparent that these sums do not differ significantly from zero and hence there is no evidence for significant interaction among groups. This result further

Table 6.-Tests of whether interaction between cluster analysis species groups have a significant effect on total bottom fish yield from the Maui-Lanai-Kahoolawe-Molokai bank.

| Term | Parameters | Evaluated <br> value | $95 \%$ confidence <br> limits |
| :---: | :---: | ---: | :---: |
| $\left(c_{1}+c_{2}\right) N_{1} N_{2}$ | $\left(c_{1}+c_{2}\right)$ | 0.242 | $(-0.244,0.728)$ |
| $\left(c_{2}+c_{3}\right) N_{2} N_{3}$ | $\left(c_{2}+c_{3}\right)$ | 0.185 | $(-0.284,0.654)$ |
| $\left(c_{1}+c_{3}\right) N_{1} N_{3}$ | $\left(c_{1}+c_{3}\right)$ | -0.868 | $(-2.365,0.629)$ |

supports the classification of species into independent assemblages for use in an aggregated treatment of the data.
In the final analysis all species were treated as a single group and the TBSM was applied to the total aggregate. Of the four possible regressions of CPUE on $f$, both the MLKM and Oahu banks yielded significant results (Table 7). Similar computations were performed for these sites as had been done previously. In addition the regression of total bottom fish CPUE on $f$ for the MLKM bank and the corresponding catch curve (catch versus effort) were plotted (Fig. 3). It is reassuring to note that the sum of the threespecies group MSY's from this bank, calculated from the preceding analysis, amounts to 103,700 $\mathrm{kg} / \mathrm{yr}$. This estimate compares favorably with the present result (a difference of about $2 \%$ ) though the two figures were computed somewhat independently. A comparison of MSY/nmi 100fathom isobath between these two banks reveals the Oahu value to be substantially less than the MLKM value. Although this may in actuality represent differences in habitat quality and productivity between these banks, there is the possibility that the difference is at least partially due to a difference in the extent of unreported recreational fishing pressure between the banks.

The results of the stock-production analysis for the MLKM bank provide statistically acceptable regressions, yet the estimates of production are

Table 7.-Significant applications of the total biomass Schaefer model to the Hawaii Division of Fish and Game data set where all species have been grouped into one total aggregate.

|  | Bank |  |
| :--- | :---: | :---: |
|  | MLKM ${ }^{1}$ | Oahu |
| MSY ${ }^{2}$ (kg/yr) | 106,000 | 15,700 |
| Optimum effort (fisherman-days) | 901 | 424 |
| MSY/nmi, 100-fathom isobath | 272 | 105 |
| Catchability coefficient | 0.00080 | 0.00168 |
| $t$ value (df = 18) | -7.77 | -2.59 |
| MLKM = Maui-Lanai-Kanoolawe-Molokai. |  |  |



Figure 3.-Fitted production curves of CPUE and catch on fishing effort for the total aggregate landings of commercial bottom fish species from the Maui-Lanai-Kahoolawe-Molokai bank.
probably low. The HDFG data provide information on only a portion of the harvest of these species. Recreational bottom fishing is very popular around the main islands of the Hawaiian Archipelago but its relative impact is completely unknown. Furthermore, underreporting by commercial fishermen is also likely but its extent is hard to determine. Based on these considerations, the overall estimate of annual production calculated for the MLKM bank ( 272 kg bottom fish $/ \mathrm{nmi} 100$-fathom isobath) is best considered a lower bound for the surplus production obtainable from this type of fishery. In spite of the difficulty in determining precise estimates of productivity it would appear that the added effects of commercial and recreational fishing are close to fully exploiting the fishery (Fig. 3). In 1978 over 96 t (metric tons) of bottom fish were harvested from the MLKM bank by commercial fishermen.

## DISCUSSION

## Fishing Effort

One of the primary goals of this study has been to estimate the commercial productivity of Hawaii's offshore bottom fish resources. We have met with mixed success in our attempt because
only one of the four study banks (Fig. 2) consistently provided significant results. In spite of this difficulty the MLKM is the largest of the four, producing well over half the total catch of bottom fish. The lack of statistical significance from the remaining banks may be due to several factors.

The impact of fishing is measured by correlating changes in fishing effort with catch rate (CPUE). If the observed range of fishing effort is too small to render an appreciable change in stock density then the impact of fishing cannot be measured. This hypothesis of insufficient variation in fishing mortality does not explain the lack of correlation between CPUE and effort from the Hawaii, Oahu, and KNK banks, however. The range in fishing intensity (defined as fisherman-days/nmi 100fathom isobath or fishing effort per unit area) between the period 1959 and 1978 was the least for the MLKM bank where only a threefold difference in intensity was experienced. In contrast, fishing intensities ranged upwards from 4 -fold (KNK) to 26 -fold (Oahu) among the remaining banks. The range of fishing intensity to which the MLKM bank has been exposed is the least of all four sites and from this observation it would be reasonable to assume that all banks have experienced substantial variation in fishing mortality.
This follows logically only if the catchability coefficients for all banks are similar. It is probable, however, that these four regions differ with respect to the impact of one unit of fishing effort on the various stocks. If differences in fishable area are corrected for, a fisherman-day recorded from Oahu may well represent less fishing mortality than the same figure from the MLKM bank. In this regard, preliminary analyses based on fishing intensity rather than fishing effortshowed that significant differences exist among the four banks in the relationship of CPUE to fishing intensity, precluding the option of pooling the data across banks (see Munro 1978 for a production analysis based on fishing intensity). In principle then, differences in catchability could explain the poor results from Hawaii, Oahu, and KNK if the catchability coefficient equating fisherman-days to fishing mortality from these areas is substantially less than that for MLKM. Variation in the extent of unreported catch among banks could compound this effect.
Other factors which remain unaccounted for
could further confound the interpretation of effort statistics. It is unknown whether the percentage of reported catch to total catch, among both commercial and recreational fishermen, is increasing, decreasing, or remaining stable. There has also been a trend toward increased fishing power with the advent of mechanical line haulers, but the exact amount of this effect is unknown. Considerations such as these make it difficult to quantify bottom fish effort statistics.

This brief discussion underscores the importance of employing an appropriate measure of fishing effort in which catchability does not vary according to the activities of man. It was possible to demonstrate the superiority of fishermandays over catch records and yet the former measure proved to be inadequate when pooling across banks was attempted.

## Effects of Aggregation

Investigators have reported that in a multispecies fishery the TBSM when applied to aggregated data often fits better than the Schaefer model applied on a species-by-species basis (FAO 1978; Pauly 1979; Pope 1979). We will examine this phenomenon for data from the MLKM bank for two levels of aggregation.

As shown in the results section we have applied the Schaefer model to CPUE and effort data at three levels of data aggregation. First we applied the Schaefer model to the data on a species-by-species basis. Then species were partitioned into three cluster groups, the catch and effort data were computed for each group, and the TBSM was fitted to each group. Finally all species were pooled into one group and the aggregate data consisting of total catch and effort were computed and fitted with the TBSM.

The fit of the TBSM to each of the three species groups and to the total group resulted in significant regressions for the MLKM bank while only 2 out of 13 single-species regressions for this bank were significant. This result may be due to the fact that the fishery exploits groups of species simultaneously and that our measure of fishing effort measures exploitation on species groups rather than single species. It is apparent that when the data in this study were progressively pooled, the correlation coefficients describing the fit became increasingly negative (Fig. 4). This result alone would suggest that aggregation led to a better fit. Unfortunately be-


Figure 4.-Frequency distributions of correlation of coefficients between CPUE and fishing effort based on three levels of species aggregation.
cause only 2 out of the 13 single-species regressions were signficant, it is not appropriate to use the single-species results in our comparison of the effects of aggregation. Table 4 presents the correlation coefficients between CPUE and effort for each of the three cluster groups and the total aggregate. At first glance it appears that for the MLKM bank the TBSM applied to the total group fits substantially better ( $r^{2}=0.77$ for fisherman-days) than the TBSM applied to any of the three species groups ( $r^{2}=0.25, r^{2}=0.59$, and $r^{2}=0.25$ ). However, an examination of the correlations between fishing effort for the three cluster groups reveals that these variables are highly correlated (Table 8). Grunfeld and Griliches (1960) have cogently argued that increased colinearity of independent variables can lead to an increase in the goodness of fit $\left(r^{2}\right)$ when data have been aggregated. This deceptive gain in the explanatory power of an aggregated independent variable prevents a direct compari-

Table 8.-Correlations of fishing effort (fishermandays) (f) among cluster analysis species groups.

| Group |  |  |  |
| :---: | :---: | :---: | :---: |
| effort | $f 1$ | $f 2$ | $f 3$ |
| $f 1$ | 1.000 | $0.943^{* *}$ | $0.900^{* *}$ |
| $f 2$ | - | 1.000 | $0.940^{* *}$ |
| $f 3$ | - | - | 1.000 |
| $*$ Significant $P=0.01, \mathrm{df}=78$. |  |  |  |

son of the coefficients of determination obtained from different levels of grouping. Thus it is improper to compare the goodness of fit for the grouped analysis to that for the total aggregate without correcting for this bias. They suggest that a more appropriate and direct way of comparing the effect of these two levels is to compare the proportion of variance in the total catch explained by the predicted total catch from the two levels of aggregation. We must use catch rather than CPUE as the dependent variable because the sum of the CPUE values predicted from each of the grouped models will not predict total CPUE.

When annual catch ( $C$ ) rather than CPUE is used the Schaefer model becomes

$$
\begin{equation*}
C=a f-b f^{2}+E \tag{2}
\end{equation*}
$$

where $a$ and $b$ are constants, $f$ is fishing effort in fisherman-days, and $E$ is a normal random variable with mean 0 and finite variance. In the case when catch and effort are aggregated into the three species groups there will be three equations of the form of Equation (2) based on the grouped annual catch ( $C_{i}$ ) and grouped annual effort ( $f_{i}$ ) for $i=1,2,3$. For the completely aggregated TBSM there will be a single equation of the form of Equation (2) with total annual catch ( $T C$ ) and total annual effort ( $T f$ ). In all four equations the nonlinear regression coefficients $a$ and $b$ can be estimated with the 20 yr of annual data from 1959 to 1978 . We can then use these coefficients to obtain predicted group annual catches $\left(\hat{C}_{i}\right)$ for groups $i=1,2,3$ and years $j=1,2, \ldots, 20$, and the predicted total annual catches ( $T C_{j}$ ) for years $j=1,2, \ldots, 20$ given the corresponding effort statistics.

We now have two estimates of total annual catch based on either $T C_{j}$ from the fully aggregated TBSM or $\hat{C}_{1 j}+\hat{C}_{2 j}+\hat{C}_{3 j}$ from the three species groups regressions. We can compare these two levels of aggregation based on their accuracy in predicting TC. This is done by defining $S S_{g}$ to be the sum of squares of $T C_{j}-C_{i_{j}}$ $-\hat{C}_{2}-C_{3 j}$ for $j=1,2, \ldots, 20$, or the deviations of the grouped predicted catch from the observed total, and defining $s_{g}{ }^{2}=S S_{g} / 19$. Let $S S_{t}$ be the sum of squares of $T C_{j}-T C_{j}, j=1,2, \ldots, 20$, or the deviations of the predicted total catch of the completely aggregated TBSM from the observed total catch. Finally let $s_{t}^{2}=S S_{t} / 19$ and $s_{T C}{ }^{2}$ be the sample variance of the total annual catch. Then the proportion of the variance of the total
annual catch explained by the sum of the three species groups model is $r_{g}{ }^{2}$ defined as:

$$
\begin{equation*}
r_{g}{ }^{2}=1-s_{g}^{2} / s_{T C}{ }^{2} \tag{3}
\end{equation*}
$$

and the proportion of the variance in the total annual catch explained by the TBSM is $r_{t}{ }^{2}$ defined as:

$$
\begin{equation*}
r_{t}^{2}=1-s_{t}^{2} / s_{T C}^{2} . \tag{4}
\end{equation*}
$$

For the MLKM bank we determine $r_{t}^{2}=0.14$ and $r_{g}{ }^{2}=0.18$. Thus the increased level of data aggregation going from treating the fishery as three separate groups to one total group does not in fact improve the fit of the catch curve although this appeared to be the case when the $r^{2}$ for the TBSM applied to the total group was compared to the $r^{2}$ values for the TBSM applied to each of the three cluster groups (Table 4, Fig. 4). As outlined previously these coefficients of determination, as calculated above, refer to the prediction of catch from effort data, for which the fit is substantially poorer than the fit of CPUE on effort.

A consideration of statistical aggregation theory has shown that the classification of bottom fish species into cluster groups results in slightly better predictions of total bottom fish catch than does analysis of the total aggregate. Since superior performance is achieved at an intermediate level of aggregation, it is possible to discount the undesirable effects of "averaging" which have troubled previous investigators (FAO 1978; Pauly 1979; Pope 1979). Furthermore, the lack of significant interaction among the species groups (Table 6) suggests that this particular application of the TBSM to the Hawaiian offshore handline fishery is appropriate.

Even though the separation of data from the MLKM bank into three species groups produced only a marginally better fit than the total aggregate model and the extra computations which are necessary were extensive (e.g., clustering), some advantage can be gained by splitting the fishery up into the groups listed in Table 3. Not only is the biological realism of the stock-production analysis enhanced but interesting patterns are also allowed to emerge. Notice, for example, that while the estimate of MSY for Group I from the MLKM bank is less than that for Group III from the same bank (Table 5), the fishing effort required to reach that figure is
substantially greater, in spite of the fact that the catchability coefficient for Group I is greater than for Group III. This apparent contradiction can be understood when estimates of carrying capacity and instantaneous growth rate are computed for the two groups. Ricker (1975) showed that the virgin shock biomass ( $B_{\infty}$ ) is equal to $a / q$ and the intrinsic rate of natural increase ( $r$ ) is equal to $a q / b$, where $q$ is the catchability coefficient and $a$ and $b$ are the intercept and slope, respectively, of the regression of CPUE on effort. Using these equations the estimate of virgin biomass for Group I at the bank is much less than for Group III whereas the intrinsic rate of natural increase for Group I is nearly double that of Group III, hence, the disparity in catchability coefficients. This manner of evaluating the growth dynamics of the fishery implies that if fishing were to stop abruptly, Group I would recover to pristine levels much sooner than either Group II or III. Thus, this analysis would predict that a form of succession would occur around the MLKM bank if fishing were curtailed as a new equilibrium point was approached. Although there is little hope of manipulating the system to test this particular prediction of the model, this type of heuristic calculation can provide valuable insights concerning the consequences of different management programs.

Pope (1979) has shown that in a multispecies fishery an increase in the colinearity of effort values among species or groups will result in a more parabolic-shaped yield curve. Consequently, he argues that if fishing pressure is exerted in such a way that the fishing mortalities of the various species remain in constant ratio to one another, then the use of the TBSM is a realistic management option. He points out though, that it cannot be concluded that an MSY estimated by application of the model to actual data is anywhere near the global maximum of the system. These considerations bear directly on this study because of the high correlations of fishing effort among the three species groups. Even though MSY from the MLKM bank is estimated to be $106 \mathrm{t} / \mathrm{yr}$ it is quite possible that a substantially larger yield could be sustained if it were possible to alter the ratios of fishing mortality among the species groups. This possibility is not unrealistic because these groups seem to be for the most part spatially separated. In principle then, appropriate management action could reduce fishing effort on one group
while simultaneously increasing that on another, but at present it is impossible to speculate about what the global MSY of the MLKM bank might be.

One of the least realistic aspects of the TBSM is its inability to adequately model trophic dynamics (Pauly 1979). The addition of LotkaVolterra interaction terms to the model (Pope 1979) is a relatively simplistic attempt to deal with this problem. Pauly (1979) argued that the surplus-yield of fish predator-prey systems may be overestimated by the TBSM because of "prudent predation" by top carnivores. This theory (Slobodkin 1961) would propose that fish predators optimally harvest their fish prey, leaving little or no remaining latent productivity of the prey species for man to utilize. These arguments must impose group selectionist reasoning and suffer as a result. Nevertheless, the TBSM assumes that total stock size is greatest in a virgin state, a condition which need not be satisfied if limitation is internally imposed (May et al. 1979).

Fortunately these considerations do not detract from the value of the present analysis. The six dominant species in the fishery (opakapaka, ulua, uku, onaga, hapu'upu'u, and kahala) are all high-level carnivores and occupy a similar trophic position. No predator-prey relationship is known to exist between any of the 13 species listed in Table 1, although extensive gut content analyses of all life history stages are currently unavailable. Thus, some of the objectionable aspects of the TBSM have been minimized by not including species from different trophic levels within the same analysis. Predator-prey relationships in a fisheries context are poorly understood at present and will probably require a more dynamic construct than the TBSM is capable of offering (May et al. 1979; Pauly 1979).

## SUMMARY

Examining the HDFG catch report data shows that the commercial deep-sea handline fishery in the Hawaiian Islands is a multispecies fishery composed principally of 13 species of bottom fish, 6 of which comprise $86 \%$ of total landings. Snappers (Lutjanidae), jacks (Carangidae), and a species of grouper (Serranidae) dominate the catch, all of which are high-level carnivores.

In the main high islands of the Hawaiian Archipelago (see Figure 2) three bottom fish
species groups are recognized based on cluster analyses which measure the tendencies of the various species to appear with one another in the catch. These groups seem to segregate on the basis of depth distribution, providing convenient biological assemblages for aggregating catch statistics.

Application of the Schaefer stock-production model to this fishery on a species-by-species basis provides an inadequate description of productivity. When species are aggregated into the cluster groups and analyzed with TBSM, the results are much improved. In this regard consistently significant results and production estimates were obtained from the MLKM bank, a region which presently accounts for half of the State of Hawaii's catch. No significant interaction among these groups was detected. When all 13 species are analyzed together, the results are in agreement with the preceding analysis. Based on TBSM applied to the MLKM bank, we estimate the annual MSY of the commercial deep-sea handline fishery to be 106 t or about 272 $\mathrm{kg} / \mathrm{nmi}$ of 100 -fathom isobath. Because recreational catch is unaccounted for, these figures are considered lower bounds for the gross production obtainable from this type of fishery although currently the commercial fishery is operating close to this MSY level.

By examining the effect of aggregating catch statistics we show that the production models based on the intermediate level of catch aggregation (cluster groups) together explain slightly more of the variation in the total catch than does the production model based on the total aggregate catch in spite of a higher coefficient of determination resulting from the latter analysis. High correlations of fishing effort among cluster groups account for this nonintuitive result.

Application of the Schaefer stock-production model to catch and effort data aggregated over species can be a useful tool for the analysis of a multispecies fishery. The appropriate level of aggregation will depend on biological and geographic factors.

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## LITERATURE CITED

Andersen, K. P., and E. Ursin.
1977. A multispecies extension to the Beverton and Holt theory of fishing, with accounts of phosphorus circulation and primary production. Medd. Dan. Fisk.Havunders. (N.S.) 7:319-435.
Anderson, W. D., Jr.
1981. A new species of Indo-west Pactific Etelis (Pisces; Lutjanidae), with comments on other species of the genus. Copeia 1981:820-825.
Brander, K. M.
1977. The management of Irish Sea fisheries - A review. G.B. Minist. Agric. Fish. Food Fish. Lab. Leafl. 36, 40 p.
Brock, V. E., and T. C. Chamberlain.
1968. A geological and ecological reconnaissance off western Oahu, Hawaii, principally by means of the research submarine "Asherah." Pac. Sci. 22:373-394.
Brown, B. E., J. A. Brennan, M. D. Grosslein, E. G.
Heverdahl, and R. C. Hennemuth.
1976. The effect of fishing on the marine finfish biomass in the Northwest Atlantic from the Gulf of Maine to Cape Hatteras. Int. Comm. Northwest Atl. Fish. Res. Bull. 12:49-68.
Dixon, W. J. (editor). 1977. BMD biomedical computer programs, P-series. Univ. Calif. Press, Los Angeles, 880 p.
FAO
1978. Some scientific problems of multispecies fisheries. Report of the expert consultation on management of multispecies fisheries, Rome, 20-23 September 1977. FAO Fish. Tech. Pap. 181, 42 p.
Fox, W. W., Jr.
1975. Fitting the generalized stock production model by least-squares and equilibrium approximation. Fish. Bull., U.S. 73:23-37.
Gosline, W. A., and V. E. Brock.
1960. Handbook of Hawaiian fishes. Univ. Hawaii Press, Honolulu, 372 p.
Grigg, R. W., and R. T. Pfund (editors).
1980. Proceedings of the Symposium on Status of Resource Investigations in the Northwestern Hawaiian Islands, April 24-25, 1980, University of Hawaii, Honolulu, Hawaii. Sea Grant Misc. Rep., UNIHI-SEAGRANT-MR-80-04, 333 p.
Grunfeld, Y., and Z. Griliches.
1960. Is aggregation necessarily bad? Rev. Econ. Statist. 42:1-13.
Gulland, J. A.
1972. Population dynamics of world fisheries. Wash. Sea Grant Publ. 72-1, Univ. Wash., Seattle, 336 p.
1974. The management of marine fisheries. Univ. Wash. Press, Seattle, 198 p.
Hawail Department of Land and Natural Resources. 1979. Hawaii fisheries development plan. Department of Land and Natural Resources, State of Hawaii, 297 p.

Larkin, P. A.
1963. Interspecific competition and exploitation. J. Fish. Res. Board Can. 20:647-678.
1966. Exploitation in a type of predator-prey relationship. J. Fish. Res. Board Can. 23:349-356.
May, R. M., J. R. Beddington, C. W. Clark, S. J. Holt, and R. M. Laws.
1979. Management of multispecies fisheries. Science (Wash., D.C.) 205:267-277.
Munro, J. L.
1978. Actual and potential fish production from the corraline shelves of the Caribbean Sea. In H. B. Stewart, Jr. (editor), Cooperative investigations of the Caribbean and adjacent regions - II. Symposium on progress in marine research in the Caribbean and adjacent regions, held in Caracas, 12-16 July 1976. Papers on fisheries, aquaculture and marine biology, p. 301-321. FAO Fish. Rep. 200.
Parrish, J. D.
1975. Marine trophic interactions by dynamic simulation of fish species. Fish. Bull., U.S. 73:695-716.
Paulik, G. J., A. S. Hourston, and P. A. Larkin.
1967. Exploitation of multiple stocks by a common fishery. J. Fish. Res. Board Can. 34:2527-2537.
Pauly, D.
1979. Theory and management of tropical multispecies stocks: A review, with emphasis on the Southeast Asia demersal fisheries. ICLARM Stud. Rev, 1, 35 p .

## Pope, J.

1979. Stock assessment in multispecies fisheries, with
special reference to the trawl fishery in the Gulf of Thailand. South China Sea Fish. Develop. Coord. Programme, SCS/DEV/79/19, 106 p.
Regier, H. A.
1980. Sequence of exploitation of stocks in multispecies fisheries in the Laurentian Great Lakes. J. Fish. Res. Board Can. 30:1992-1999.
Ricker, W. E.
1981. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191, 382 p.
Rothschild, B. J.
1982. Fishing effort. In J. A. Gulland (editor), Fish population dynamics, p. 96-115. Wiley, Lond.
Sale, P. F.
1983. Maintenance of high diversity in coral reef fish communities. Am. Nat. 111:337-359.
SAS Institute.
1984. SAS user's guide. 1979 ed. Statist. Anal. Syst., 494 p.
Slobodkin, L. B.
1985. Growth and regulation of animal populations. Holt, Rinehart, and Winston, N.Y., 184 p.
Strasburg, D. W., E. C. Jones, and R. T. B. Iversen.
1986. Use of a small submarine for biological and oceanographic research. J. Cons. 31:410-426.
talbot, F. H., B. C. Russell, and G. R. V. Anderson.
1987. Coral reef fish communities: unstable, highdiversity systems? Ecol. Monogr. 48:425-440.

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    ${ }^{2}$ Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 3830, Honolulu, HI 96812.

[^1]:    ${ }^{3}$ Laevastu, T., and F. Favorite. 1978. Numerical evaluation of marine ecosystems. Part 1. Deterministic bulk biomass model (BBM). NWAFC Process. Rep., Natl. Mar. Fish. Serv., NOAA, Seattle, Wash., 22 p. (Unpubl. rep.)

[^2]:    ${ }^{4}$ Ralston. S. 1979. A description of the bottomfish fisheries of Hawaii, American Samoa, Guam, and the Northern Marianas. A report submitted to the Western Pacific Regional Fishery Management Council, Honolulu, 102 p. (Unpubl. rep.)

[^3]:    ${ }^{5}$ R. N. Uchida, Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812, pers. commun. November 1980.

