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A VARIABLE CATCHABILITY VERSION OF THE LESLIE MODEL WITH APPLICATION TO AN INTENSIVE FISHING EXPERIMENT ON A MULTISPECIES STOCK

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ABSTRACT

A variable catchability version of the Leslie model is developed which permits the catchability of one species to vary inversely with the abundance of competing species. This model is used to fit data from an intensive fishing experiment conducted on a multispecies bottom fish stock in the Marianas where catchability of a subordinate species is inversely related to the abundance of a more dominant species. Analysis of this multispecies intensive fishing experiment produced estimates of exploitable bottom fish density in the 150-275 m depth range of 10,156 fish per nmi^2 or 1,354 fish per nmi of 183 m (100-fathom) contour.

Intensive fishing of a closed population can produce data to estimate the initial population size and the catchability coefficient of fish stocks. Two frequently used models applied to intensive fishing data are the Leslie model and the Delury model (Ricker 1975). The Leslie model expresses catch per unit effort (CPUE) at any point during the period of intensive fishing as a linear function of the cumulative catch to that point, whereas the Delury model expresses the logarithm of CPUE at any point during the intensive fishing experiment as a linear function of the cumulative effort. From a statistical viewpoint the Leslie model is often preferable to the Delury model, since a predictive linear regression is used to estimate the parameters of both models and since typically catch is measured more accurately than effort.

Both the Leslie and Delury models assume that catchability is constant during the period of intensive fishing. However, experience indicates that this assumption may not always be satisfied (Pope and Garrod 1975; Schaaf 1975; MacCall 1976; Ulltang 1976; Garrod 1977; Peterman and Steer 1981; Fox[2]). Several authors have found that competition for baits between fish of different size or species can alter catchability (Allen 1963; Rothschild 1967). In this paper a variable catchability Leslie model will be developed for multispecies application where, due to species interactions, the catchability of one species is altered by the presence of other species. This variable catchability Leslie model will be applied to multispecies intensive fishing data from snapper (family Lutjanidae) populations where the application of the constant catchability Leslie model leads to biologically untenable results.

VARIABLE CATCHABILITY LESLIE MODEL

The CPUE during a time interval t (CPUE(t)) is defined as the product of catchability (q) and the mean population size (number of individuals) present during the period t ($N(t)$), thus

$$\mathrm{CPUE}(t) = qN(t). \tag{1}$$

Suppose that up to the beginning of period t, $K(t)$ fish have been caught and removed. If the period t is relatively short, the population of fish closed or isolated, and the fishing pressure heavy enough so that it can be assumed that mortality from other factors is negligible, then $N(t)$ can be expressed as

$$N(t) = N(0) - K(t),$$

where $N(0)$ is the initial population size at the beginning of the experiment ($t = 0$). Inserting this expression for $N(t)$ in Equation (1) produces the Leslie model:

$$\mathrm{CPUE}(t) = q(N(0) - K(t)). \tag{2}$$

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[2]Fox, W. W. 1974. An overview of production modelling. U.S. National Marine Fisheries Service, Southwest Fisheries Center, Administrative Report LJ-74-10, La Jolla, CA.

Manuscript accepted August 1985.
FISHERY BULLETIN: VOL. 84, NO. 2, 1986.

Henceforth, this model will be referred to as the constant catchability Leslie model.

In a multispecies situation, competition between species for baited hooks may produce a dominance hierarchy where some species are more aggressive feeders than others and effectively out compete the less aggressive feeders for baited hooks. The catchability of the species at the top of the dominance hierarchy, is independent of the presence of more subordinate species, while the catchability of those species not at the very top of the hierarchy will vary inversely with the abundance of the more dominant species. A simple model which describes the catchability of a subordinate species ($q(s,t)$) as a function of the cumulative catch and initial population size of the more dominant species, $K(d,t)$ and $N(d,0)$ respectively is

$$q(s,t) = q(s)(K(d,t)/N(d,0)) \qquad (3)$$

where $q(s)$ is the catchability of the subordinate species in the absence of the dominant species. Combining Equations (2) and (3) produces

$$\mathrm{CPUE}(s,t) = q(s)(K(d,t)/N(d,0)) \times (N(s,0) - K(s,t)) \qquad (4)$$

and by defining $K(ds,t) = K(d,t)K(s,t)$, $B1 = q(s)(N(s,0)/N(d,0))$, and $B2 = q(s)/N(d,0)$ Equation (3) becomes

$$\mathrm{CPUE}(s,t) = B1K(d,t) - B2K(ds,t).$$

Estimates of $B1$ and $B2$ are obtained from multiple linear regression and the estimates of $N(s,0)$ and $q(s)$ are computed as

$$\hat{N}(s,0) = \hat{B}1/\hat{B}2, \text{ and } \hat{q}(s) = \hat{N}(d,0)\hat{B}2.$$

The estimate of $N(d,0)$ is determined from the constant catchability model. As is evident from Equation (4), the estimate of $N(s,0)$ is independent of the estimate of $N(d,0)$. Estimates of the variance of the estimate of $N(s,0)$ are obtained from estimates of the means and variances of the estimates of $B1$, and $B2$ and an exact expression for the variance of a ratio (Frishman 1975). Thus,

$$V(\hat{N}(s,0)) = V(\hat{B}1/\hat{B}2) = \frac{V(\hat{B}1)[E(\hat{B}2)]^2 - V(\hat{B}2)[E(\hat{B}1)]^2}{(E(\hat{B}2))^2\,[V(\hat{B}2) + [E(\hat{B}2)]^2]} \qquad (5)$$

where $V(\ )$ and $E(\ )$ represent the variances and means, respectively.

APPLICATION OF MULTISPECIES LESLIE MODEL TO SNAPPER INTENSIVE FISHING

A 13-d intensive fishing experiment covering the period 10-19 April and 5-7 May 1984 was conducted at Pathfinder Reef (lat. 16°30′N, long. 143°05′E) in the Mariana Archipelago. Pathfinder Reef is a circular pinnacle rising steeply from a depth of about 1,600 to 16 m beneath the surface. At the 200 m contour, the diameter is about 0.8 nmi (Fig. 1). The snapper population at Pathfinder Reef is a closed population for purposes of the intensive fishing since the closest bank is a small pinnacle 40 nmi to the north.

Intensive fishing was conducted from the NOAA ship *Townsend Cromwell* using four bottom handlines on hydraulic gurdies targeting species in the 150-275 m depth range. Each day during the 13-d experiment, fishing was conducted around the entire perimeter of the bank. During the experiment 1,467 bottom fish were caught. Three lutjanids, *Pristipomoides zonatus*, *P. auricilla*, and *Etelis carbunculus*, accounted for 1,317 fish or about 90% of the catch (Table 1). Fishing effort was measured in

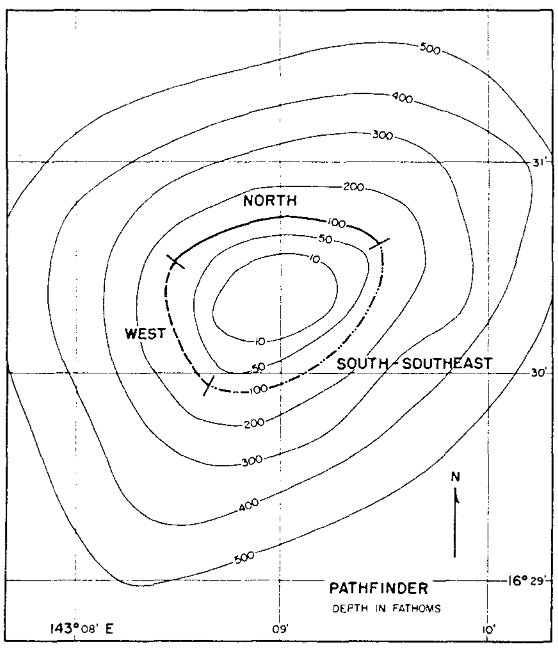

FIGURE 1.—Bathymetric chart of Pathfinder Reef showing the segments of the 100-fathom (183 m) contour used to partition daily fishing effort.

TABLE 1.—Species composition of bottom fish catch at Pathfinder Reef.

Species	Number caught	Percent of catch
Lutjanidae		
Aphareus rutilans	4	0.27
Aprion virescens	1	0.07
Etelis carbunculus	314	21.40
Pristipomoides auricilla	262	17.86
P. filamentosus	16	1.09
P. flavipinnis	7	0.48
P. zonatus	741	50.51
Carangidae		
Caranx lugubris	83	5.66
Seriola sp.	32	2.18
Serranidae		
Cephalopholis igarasiensis	2	0.14
Epinephelus cometae	2	0.14
Saloptia powelli	3	0.20
Total	1,467	100.00

line-hours. As is indicated in Figure 1, the circumference of the reef can be divided into three segments—north, west, and south-southeast, each having similar species composition (Table 2). Further, an attempt was made daily to allocate a consistent proportion of the day's fishing effort to each segment. The proportion allocated to each segment was influenced by the length of each segment and wind and current conditions. On the average, the proportion of the total daily effort allocated to each segment was 0.45 on the south-southeast, 0.21 on the north, and 0.34 on the west. A chi-squared test applied to the daily allocation of fishing effort indicates that there was no significant departure ($P = 0.89$) from this allocation during the course of the fishing experiment. Since the effort was reasonably constant over the duration of the experiment and the entire reef was fished each day, catch, effort, and CPUE computed on a daily basis were used in the analysis. An adjustment to cumulative catch suggested by Chapman (1961) was subsequently shown to improve the model fit in the Delury model (Braaten 1969). This adjustment computes cumulative catch for interval i as the cumulative catch to interval i plus one half the catch during interval i. This adjustment compensates for the decline in CPUE within each time interval. The adjusted cumulative catch is used as the independent variable in all subsequent analyses (Table 3).

TABLE 2.—Species composition for the three segments of the circumference of Pathfinder Reef (see Figure 1).

Species	South-Southeast No.	South-Southeast %	North No.	North %	West No.	West %
Pristipomoides zonatus	358	51	160	68	223	58
P. auricilla	170	24	37	16	55	14
Etelis carbunculus	171	25	39	17	104	27

Plots of CPUE against adjusted cumulative catch for each of the three species of snappers show a decline in CPUE for *P. zonatus*, a slight decline for *E. carbunculus*, and an increase for *P. auricilla* (Fig. 2). A regression line fitted to these data results in negative slopes for *P. zonatus* ($P = 0.0007$) and *E. carbunculus* ($P = 0.05$) and a positive slope for *P. auricilla* ($P = 0.008$). The constant catchability Leslie model fitted the *P. zonatus* data well and resulted in an R^2 of 0.71 and a pattern of residuals which supports the linear model. The estimates of $N(0)$ and q for *P. zonatus* from this fit are 1,066 fish and 0.0038 per line-hour. Due to the selectivity of the fishing gear, $N(0)$ estimated from this intensive fishing data does not represent total population size

TABLE 3.—Daily catch, effort, catch per unit of effort (CPUE), and adjusted cumulative catch for *Pristipomoides zonatus*, *P. auricilla*, and *Etelis carbunculus*

Date 1984	Effort (line-hours)	Total Catch (no.)	Total CPUE	Total Adjusted cumulative catch	*P. zonatus* Catch (no.)	*P. zonatus* CPUE	*P. zonatus* Adjusted cumulative catch	*P. auricilla* Catch (no.)	*P. auricilla* CPUE	*P. auricilla* Adjusted cumulative catch	*E. carbunculus* Catch (no.)	*E. carbunculus* CPUE	*E. carbunculus* Adjusted cumulative catch
Apr. 10	27.5	152	5.53	76	98	3.56	49	12	0.44	6	42	1.53	21
Apr. 11	23.7	150	6.33	227	111	4.68	153.5	17	0.72	20.5	22	0.93	53
Apr. 12	21.3	100	4.67	352	47	2.21	232.5	12	0.56	35	41	1.93	84.5
Apr. 13	29.7	139	4.68	471.5	91	3.06	301.5	29	0.98	55.5	19	0.64	114.5
Apr. 14	29.3	112	3.82	597.0	66	2.25	380	17	0.58	78.5	29	0.99	138.5
Apr. 15	17.5	84	4.80	695.0	50	2.86	438	13	0.74	93.5	21	1.20	163.5
Apr. 16	30.7	129	4.20	801.5	67	2.18	496.5	26	0.85	113	36	1.17	192.0
Apr. 17	21.4	65	3.04	897.5	38	1.78	548	12	0.56	132	15	0.70	217.5
Apr. 18	22.4	81	3.62	970.5	41	1.83	587.5	15	0.67	145.5	25	1.12	237.5
Apr. 19	21.6	60	2.78	1,041	28	1.30	622.0	17	0.78	161.5	15	0.69	257.5
May 5	20.3	82	4.04	1,112.5	40	1.97	656	29	1.43	184.5	13	0.64	271.5
May 6	22.8	91	3.99	1,199.0	35	1.54	693.5	35	1.54	216.5	21	0.92	288.5
May 7	24.1	72	2.99	1,281	30	1.25	726.0	27	1.12	248.5	15	0.62	306.5

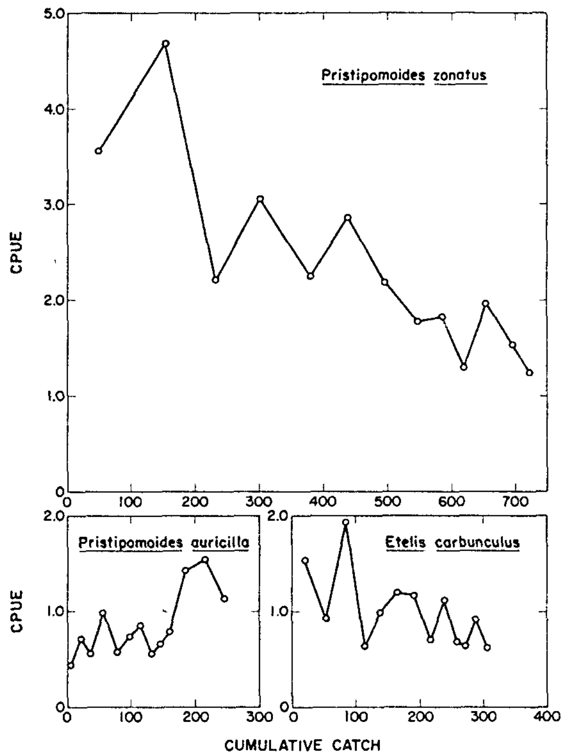

FIGURE 2.—Daily catch per unit effort (CPUE) and adjusted cumulative catch for *Pristipomoides zonatus, P. auricilla,* and *Etelis carbunculus.*

but rather the population size of those fish that can be caught by the fishing gear which will be termed the exploitable population. Although the constant catchability Leslie model does not explain as much of the variation for *E. carbunculus* (R^2 = 0.35) as it does for *P. zonatus*, the regression is significant and the pattern of residuals supports the linear fit. The estimates for catchability and initial exploitable population size for *E. carbunculus* from the fit of this model are 0.0025 per line-hour and 583 fish. The positive slope for the regression of CPUE on cumulative catch for *P. auricilla* does not make sense biologically under the constant catchability Leslie model.

The depth of capture data show that *P. zonatus* and *P. auricilla* were caught in the same depth range, whereas *E. carbunculus* was typically caught at somewhat greater depths (Table 4). Thus, species interactions would most likely occur between *P. zonatus* and *P. auricilla*. If *P. zonatus* is more aggressive than *P. auricilla* in pursuing fishing baits or in some other way affects the behavior of the latter, then the initial catchability for *P. auricilla* will

TABLE 4.—Percent of catch by depth (in fathoms, 1 fathom = 1.83 m).

Species	Depth <100	100-120	>120
Pristipomoides zonatus	15.1	71.7	13.2
P. auricilla	12.6	79.0	8.4
Etelis carbunculus	1.9	46.5	51.6

be low but will rise as the population of *P. zonatus* is reduced. Applying the variable catchability Leslie model to the *P. auricilla* data, with the assumption that *P. zonatus* is the dominant species and that *P. auricilla* is the subordinate species so that the catchability of *P. auricilla* depends on the population size of *P. zonatus*, results in the following relationship:

$$\mathrm{CPUE}(a,t) = q(a)(K(z,t)/N(z,0)) \times (N(a,0) - K(a,t)), \qquad (6)$$

where $q(a)$ is the catchability of *P. auricilla* in the absence of *P. zonatus* and $N(z,0)$ and $N(a,0)$ are the initial exploitable population sizes of *P. zonatus* and *P. auricilla*, respectively, and $K(z,t)$ and $K(a,t)$ are the cumulative catch of *P. zonatus* and *P. auricilla* to time t, respectively.

Using the estimate of $N(z,0)$, 1,066 fish, from the fit of the constant catchability model to *P. zonatus* data, Equation (6) has two unknowns to be estimated—$q(a)$ and $N(a,0)$. A multiple linear regression model estimates the initial exploitable population size of *P. auricilla*, $N(a,0)$, at 2,007 fish and $q(a)$ at 0.00087. The variable catchability Leslie model fits the *P. auricilla* CPUE data well and produces an R^2 of 0.89 (Fig. 3). The estimates of initial population sizes for the three species are summarized in Table 5 together with their 95% confidence intervals. For the constant catchability model, the population size confidence interval is computed from a relationship derived by Delury (1958), whereas the confidence interval for the variable catchability model is computed from the variance expression given in Equation (5).

DISCUSSION

The constant catchability Leslie model fit the *P. zonatus* and *E. carbunculus* data well but was not appropriate for the *P. auricilla* data. The variable catchability Leslie model fit the *P. auricilla* data well and provided a plausible explanation for the observed increase in CPUE. Given that there was a time delay between the first 10 d of the intensive fishing (10-19 April) and the last 3 d (5-7 May), and that the greatest increase in the catchability of *P. auricilla* occurred after the time delay, it is possible that the increase in catchability might have a time lag component associated with it. However, given the short time series of data, it would be difficult to test the appropriateness of a more complicated time lag model.

Based on the fit of these two models the initial exploitable population of the three species in the 150-275 m depth range at Pathfinder Reef is estimated at 3,656 fish (Table 5). If we assume, based on the species composition data (Table 1), that these three species represent 90% of the exploitable population then the total exploitable population at the beginning of the intensive fishing is 4,062 fish.

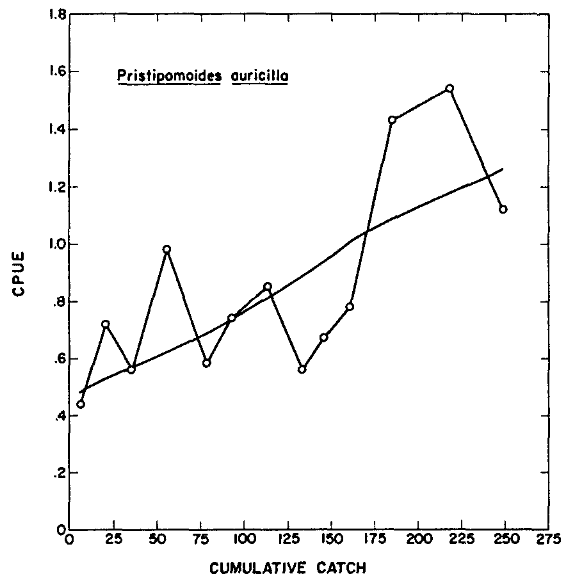

FIGURE 3.—Daily catch per unit effort (CPUE) and predicted CPUE based on the variable Leslie model as a function of adjusted cumulative catch for *Pristipomoides auricilla*.

From Figure 1 the length of the 183 m (100-fathom) contour is estimated at 3.0 nmi, and the area in the 180-300 m depth range is estimated to be 0.4 nmi^2. With these area measures, density estimates of 1,354 fish per nmi of (183 m) 100-fathom contour and 10,156 fish/nmi^2, are obtained for Pathfinder Reef.

Estimates of bottom fish densities based on visual observation from a submersible at Johnston Atoll were 57,281 fish/nmi^2 for the 92-183 m (50-100 fathom) depth range and 66,199 fish/nmi^2 for the 1983-274 m (100-150 fathom) depth range (Ralston et al. 1986). These figures are considerably larger than both the point and interval estimates presented here. Significantly, the study of Ralston et al. (1986) also employed the *Townsend Cromwell*, and the catch rates were comparable at Pathfinder and Johnston (e.g., 3.18 bottom fish/line-hour for the latter). Thus the difference between estimates of standing stock is likely not due to differences in absolute abundance but rather to differences between exploitable population size and total population size. For example, at Johnston Atoll at least 69 species of fish were observed from the submersible, whereas only 10 species were taken by fishing gear in the same depth (Ralston et al. 1986).

If the constant catchability Leslie model is applied to the pooled data for the three species, an estimate of exploitable population size of 2,689 is obtained, about 71% of the estimate of the exploitable population size for the three species when they are estimated separately (Table 5).

Size-specific behavior has been raised as a factor which might affect catchability (Allen 1963). For all three species, there is no evidence of intraspecies size-specific behavior affecting catchability since for two of the species the constant catchability model fits well and for the third species, catchability depends only on the population size of an interacting species. Further, under the hypothesis that within a stock catchability is size-specific across the

TABLE 5.—Estimates of population size and catchability for three species.

Species	Model	R^2	Catch-ability	SE	Initial population size	Confidence interval (95%)
Pristipomoides zonatus	Constant catchability	0.71	0.0038	0.0075	1,066	(803-1,691)
Etelis carbunculus	Constant catchability	0.35	0.0025	0.0010	583	(361-3,011)
P. auricilla	Variable catchability	0.89	0.00087	0.00031	2,007	(261-5,727)
Three species pooled	Constant catchability	0.66	0.0022	0.0047	2,689	(1,955-4,535)

range of exploitable size, intensive fishing would produce a substantial change in the population size structure. A plot of the mean fork length by day of fishing for the three species (Fig. 4) shows very little change in fork length even for *P. zonatus* where 68% of the exploitable stock is estimated to have been removed. Thus, the mean size of the fish in a catch may be a much less sensitive indicator of changes in the population size than catch rates, at least over the short term.

ACKNOWLEDGMENTS

I wish to thank Alec D. MacCall and William E. Schaaf whose reviews resulted in an improvement in the formulation of the variable catch Leslie model. This paper is a result of the Resource Assessment Investigation of the Mariana Archipelago at the Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA.

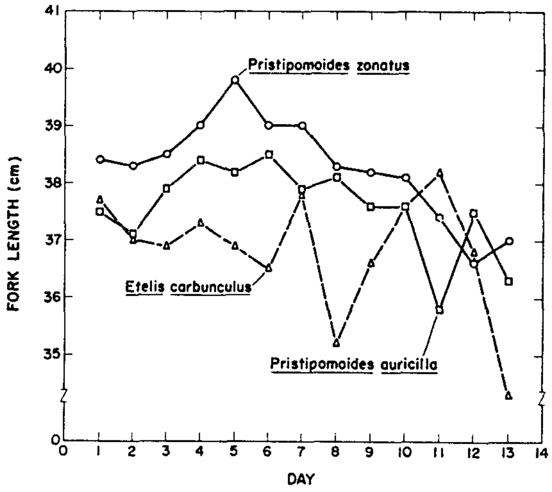

FIGURE 4.—Mean fork length for each day of fishing for *Pristipomoides zonatus*, *P. auricilla*, and *Etelis carbunculus*.

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