MAXIMUM YIELD ESTIMATES FOR THE PACIFIC THREAD HERRING, OPISTHONEMA SPP., FISHERY IN COSTA RICA

DAVID K. STEVENSON' AND FRANCISCO CARRANZA²

ABSTRACT

Linear and exponential surplus production models were applied to annual 1969-79 catch per unit effort and effort data obtained from the Costa Rican Pacific thread herring fishery. Effort was estimated as the number of calendar days at sea and standardized to account for presumed increases in fishing power and "real" fishing time (time spent searching for fish) after 1973. Independent regression analyses were performed using standardized and unstandardized effort estimates. In addition, values of the independent variable were estimated both as simple annual effort and as a moving 2-year average of effort. All regressions were statistically significant, but the best fit was obtained with standardized average effort and the exponential model. The "best" estimates of maximum equilibrium yield and effort ($Y_s = 6,430$ t; $f_s = 1,036$ days or 1,096 standard days) indicated that the resource was overexploited in 1974-75, 6 years after fishing began. In 1976-77 catch remained at approximately Y_s levels while effort remained above f_s . Catch and observed effort declined dramatically during 1978-79 although standardized effort remained slightly above 1,100 standard days. Future management of the resource may require limited catch and/or effort. The validity of the model is discussed primarily in terms of the nonindependence of the X and Y variables.

Thread herring (genus Opisthonema) are schooling pelagic clupeids which inhabit tropical and subtropical coastal waters of the western Atlantic and eastern Pacific Oceans. According to Berry and Barrett (1963), three Pacific species (Opisthonema libertate, O. bulleri, and O. medirastre) are found in continental waters between northern Mexico and Peru while a fourth species (O. berlangai) is limited to the Galapagos Islands. These authors differentiated individual species on the basis of the number of gill rakers, a meristic character which was found to be positively related to standard length. The most abundant Atlantic species (O. oglinum) is distributed from southern Brazil to the Gulf of Maine.

Thread herring school in nearshore waters (Klima 1971; Magnusson 1971) and are planktivorous feeders. Fuss et al. (1969) observed copepods and larval pelecypods, gastropods, and barnacles in the stomachs of Atlantic thread herring. Peterson (1956) reported mostly phytoplankton from Pacific thread herring stomachs collected in Costa Rica. The presence of fine sediments in the stomachs of Atlantic thread herring indicated that these fish may spend some time feeding on the bottom.

Atlantic thread herring spawn during April-August in the eastern Gulf of Mexico. Fuss et al. (1969) reported a maximum mean gonad index in June, and Houde (1976) collected eggs when surface seawater temperature ranged from 22.5° to 30° C. Most eggs and larvae were collected within 50 km of the coast. Based on the histological examination of reproductive tissue, Paez Barrera³ reported peak spawning for O. libertate in Mexico during June and July at water temperatures of 25°-29° C. Peterson (1956) collected small individuals (<60 mm SL, standard length) in the Gulf of Nicoya, Costa Rica, during all months of the years 1952-54. His observations indicated that spawning may have been continuous. Furthermore, nearly all collections of adults included some individuals which were sexually mature. Continuous recruitment on the Pacific coast of Costa Rica was also implied by the presence of a predominant size group at 18-20 cm SL in most

¹Department of Zoology, University of Maine, Orono, ME 04469 or Maine Department of Marine Resources, West Boothbay Harbor, ME 04575.

²Departamento de Estudios Biológicos de Fauna Marina y Continental, Ministerio de Agricultura y Ganadería, San Jose, Costa Rica.

³Paez Barrera, F. 1976. Desarrollo gonadal, madurez, desove y fecundidad de sardina crinuda, *Opisthonema libertate* (Gunther) de la zona de Mazatlan, basados en el analisis histológico de la gónada. Mem. del Simp. sobre Recursos Masivos de México, Ensenada, B.C., 28-30 de Septiembre de 1976, p. 207-255.

monthly length-frequency distributions compiled from commercial landings by the Costa Rican Ministry of Agriculture during 1975-77.

Attempts to determine the age and growth of *Opisthonema* spp. based on apparent scale annuli and length-frequency analyses have not produced very satisfactory results, presumably since growth rates and recruitment are more or less continuous throughout the year. Reintjes⁴ reported that few Atlantic thread herring live beyond age 4, and Sokolov and Wong⁵ speculated that there were three adult year classes of O. libertate within the harvestable size range (5-26 cm SL)in the Gulf of California. Paez Barrera (footnote 3) reported a minimum length at maturity of 13-14 cm SL for O. libertate in Mexico. Houde (1976) reported that age 1 Atlantic thread herring measured approximately 13 cm SL. Length-frequency distributions for Opisthonema spp. sampled from commercial landings in Costa Rica were commonly characterized by a single predominant size group at 18-20 cm SL, but occasionally included a second group at 12-16 cm SL.

Although he presented no information for Opisthonema, Beverton (1963) indicated that most clupeid and engraulid species are short lived (5 yr or less) and are generally characterized by high growth and mortality rates. Furthermore, these fish mature at relatively early ages (age at maturity/maximum age = 0.30-0.37) and grow very little after maturing (length at maturity/ maximum length = 0.65-0.80) compared with other taxonomic groups. High mortality rates (Z= 0.5-3.0) can be largely attributed to the active predation on these fish by man, birds, and other fish. Highly variable recruitment has contributed to the decline of many stocks of small pelagic fishes for which recruitment appears to be independent of spawning stock size over a wide range of stock sizes (Murphy 1977).

The most important thread herring fisheries are conducted on the Pacific coast of Central and South America. Most of the 1972-77 catch of Pacific thread herring was landed in Ecuador (Table 1) where landings increased by 700% during this

TABLE 1.—Annual 1972-77 landings (thousand metric tons) of Pacific thread herring in Ecuador, Panama, and Mexico. Sources: FAO Yearbook of Fishery Statistics (1979) and Instituto Nacional de Pesca, Mexico.

Country	1972	1973	1974	1975	1976	1977
Ecuador	552	050	1 100	1 750	2 250	2 930
Panama	143	205	367	201	166	234
Mexico	18	36	22	32	35	65
Total	713	1,191	1,489	1,983	2,451	4,129

6-yr period. Panama and Mexico accounted for <10% of the total reported landings in 1976 and 1977. Thread herring are harvested with the Pacific sardine, *Sardinops sagax*, in Mexico and are utilized both for human consumption and for fish meal. Thread herring are harvested incidentally to the anchoveta, *Centengraulis mysticetus*, in the Gulf of Panama and reduced to meal. Thread herring fisheries do not presently exist in any of the remaining Central American countries except Costa Rica where, by law, the total production is canned for human consumption.

Thread herring have been harvested on the Pacific coast of Costa Rica since 1968. The fleet expanded steadily from a single vessel in 1968-69 to nine vessels in 1975. At present the fleet consists of 10 vessels, although only half the fleet may be active at any one time. Most of the fish landed during 1968-73 were harvested in the outer Gulf of Nicoya (Figure 1) and from coastal waters immediately to the south. Purse seiners and trawlers have been prohibited from fishing in the interior of the Gulf of Nicoya since 1975. The fishery expanded as far south as Golfo Dulce near the Panamanian border in 1972. Total catch reached a maximum of 7,500 t in 1975 and declined to about 5,000 t in 1978 and 1979, while total catch per day at sea peaked in 1971 (Figure 2). Catch in the Gulf of Nicoya peaked at 5,000 t in 1972 (Figure 3) and at 2,800 t in Golfo Dulce during 1975 (Figure 4).

The thread herring resource supports a small but important industry in Costa Rica. Landings in 1978 accounted for 36% of all fish and shellfish landed by the domestic fleet and \$76,635 in exvessel revenue. Most of the herring canned in Costa Rica is sold domestically. A small quantity (9% in 1977) is exported to other Central American countries. There are three canning plants in the country, two in Puntarenas and one in Golfito. Eight of the existing 10 vessels are based in Puntarenas.

The objective of this study was to determine, from historical catch and effort data compiled by

⁴Reintjes, J. W. 1979. A review of the clupeoid and carangid fishery resources in the western central Atlantic. Interregional Project for the Development of Fisheries in the Western Central Atlantic (WECAF), 49 p.

⁵Sokolov, V. A., and M. I. Wong. 1973. Informe científico de las investigaciones sobre los peces pelágicos del Golfo de California (sardina crinuda y anchoveta) en 1971. Inst. Nac. Pesca, Inf. Cién. 2, 41 p.





the Costa Rican Ministry of Agriculture, the maximum equilibrium yield which this resource will support and the amount of fishing effort required to achieve complete utilization. The methodology and the simplifying assumptions used in this study were necessary given the scarcity of biological information, the absence of species-specific catch data, and the nature of

(IO3 M TONS) UNIT EFFORT 7.0 TONS / DAY AT SEA) 6,0 5.0 CATCH CATCH / 3.0 CPUF 5.0 ANNUAL 2.0 ANNUAL Σ 1.0 0. 1979 1970 1972 1974 1970 1971 YEAR

FIGURE 2.—Annual 1968-79 catch and catch per unit effort for three species of thread herring captured on the Pacific coast of Costa Rica (all zones). Catch and effort data were compiled from sales receipts.

available effort statistics, and illustrate some of the problems which impede stock assessments in developing countries.

DEFINITION OF THE UNIT STOCK

Three species of *Opisthonema* are harvested on the Pacific coast of Costa Rica. Species identifica-



FIGURE 3.—Annual 1968-79 catch and catch per unit effort data for three species of thread herring captured in the Gulf of Nicoya, Costa Rica (zone 1). Catch and effort data were compiled from captain's reports and verified from sales receipts.



FIGURE 4.—Annual 1972-79 catch and catch per unit effort data for three species of thread herring captured in the Golfo Dulce area of Costa Rica (zone 3). Catch and effort were compiled from captain's reports and verified from sales receipts.

tion is based on the relation between the number of gill rakers and standard length (Berry and Barrett 1963). Over 3,000 specimens of thread herring collected from commercial catches by the Costa Rican Ministry of Agriculture during the period April 1975 to December 1977 were separated into two groups based on external coloration and morphological features. One group ("blue sardines") consisted of fish which more easily lost their scales and which were characterized by a blue dorsal coloration and more shallow, elongated bodies. These fish were predominantly O. bulleri. The second group ("green sardines") consisted primarily of O. medirastre and O. libertate. Fish in this group retained their scales, had deeper bodies, and a greener dorsal coloration. The second group was more abundant than the first, accounting for more than 90% of the fish sampled from commercial landings except during February-July 1977 when blue sardines made up 25-63% of the samples. Since the sampling procedures used were not strictly random and exact species identifications were not attempted, it can only be concluded that O. medirastre and O. libertate appeared to be the predominant species in the catch during most of the sampling period.

In the absence of species-specific catch and effort information all three species were, for the purposes of analysis, assumed to compose a single unit stock confined to Costa Rican coastal waters. The degree to which the different species shared common growth or natural mortality rates was not known, nor was it certain whether they school together and were thus exploited with the same intensity in the same areas. Although commercial fishermen in Costa Rica have observed that O. *libertate* and O. *medirastre* intermingle in the same schools, *O. bulleri* are rarely captured together with the other two species and apparently do not school with them. Berry and Barrett (1963) reported that the size ranges of all three coastal Pacific species collected in Central and South America were nearly equal, an observation that was generally confirmed in samples taken from commercial catches in Costa Rica and which indicated that all three species were equally susceptible to capture over the same size range. All three species harvested in Costa Rica during 1975-77 reached a maximum size of about 24 cm SL.

The assumption of a single geographic stock in Costa Rican waters was largely an arbitrary one since there was no information available concerning the migratory behavior of the Pacific species. Klima (1971) reported that Atlantic thread herring, O. oglinum, in the northeastern Gulf of Mexico seldom are found in depths >100 m and are most common in depths <40 m. Similar observations have been reported for Pacific thread herring in Central America (Magnusson 1971). Kinnear and Fuss (1971) reported seasonal north-south migrations of O. oglinum on the west coast of Florida in response to changes in surface water temperatures. A southerly fall migration of 6-7 mi/d has been observed for O. oglinum between North Carolina and Florida (Pristas and Cheek 1973). Since seawater temperatures along the Pacific coast of Central America presumably are more constant, such directed migration may not occur.

Despite the fact that the three coastal Pacific species of *Opisthonema* are distributed continuously from the Gulf of California to Peru (Berry and Barrett 1963), there is some justification for treating the Costa Rican thread herring resource as a single geographic unit stock since there are no fisheries for thread herring in any of the other Central American countries except Panama. In Panama, *Opisthonema* spp. are harvested only in the Gulf of Panama and not in the intervening coastal waters of western Panama between the Gulf and the Costa Rican border.

METHODS

Estimation of Catch and Effort Statistics

Total annual catch and effort data were compiled from sales receipts obtained from the canning companies in Puntarenas and Golfito (Table 2). Catch data were reliable since the entire catch in Costa Rican waters was harvested by Costa TABLE 2.— Annual 1968-79 catch, effort, catch per unit effort, and average effort statistics for three species of thread herring captured on the Pacific coast of Costa Rica. Catch and effort data were compiled from sales receipts. Source: Oficina de Pesca, Ministerio de Agricultura y Ganadería, Puntarenas, Costa Rica.

Year	Catch (t)	f _t Effort (d at sea)	f Average effort $= \frac{1}{2}(f_t + f_t - 1)$ (d at sea)	<i>Ct/ft</i> (t/d)
1968	726	130	65	5.59
1969	2,400	200	165	12.00
1970	3,765	264	232	14.26
1971	3,323	217	240	15.31
1972	5,822	431	324	13.51
1973	4,886	501	466	9.75
1974	7,193	844	672	8.52
1975	7,592	1,304	1,074	5.82
1976	6,330	1,350	1,327	4.69
1977	6,619	1,176	1,263	5.63
1978	5,034	884	1,030	5.70
1979	4,654	753	818	6.18

Rican vessels and sold for canning in these two ports. Effort was estimated from sales receipts as the number of calendar days at sea and recorded as the difference between the dates of departure and arrival in port. One day at sea was considered to include only 12 daylight hours since no fishing was conducted at night. Effort measurements included any daylight time spent in transit to and from port, time actually spent setting and retrieving the net, time spent searching for schools of fish, and any time lost for vessel repairs or other activities unrelated to the capture of fish.

Some information on the division of total effort was available from Ministry of Agriculture biologists who observed vessel activities during five fishing trips in the Gulf of Nicoya during August and September 1980 (Table 3). During a total of 95 h absent from port, 60 h (63%) were spent searching for fish, 23 h in setting and retrieving the net, and 12 h were lost in transit and other activities unrelated to fishing. An average of 8.6 h were spent working per calendar day. The fourth trip was the most productive trip in terms of catch per day, catch per hour search, and catch per total hours, but the first and second trips were the most productive in terms of catch per hour fishing. These observations tended to confirm the assumption that search time was the most significant component of total effort and indicated that catch per day, the index of CPUE (catch per unit effort) used in this assessment, compared more closely to catch per hour search than to catch per hour fishing with the net. Although these observations were recorded for a very short period of time and did not represent average fishing conditions for the entire fishery during that time, they do give an idea of how time at sea was apportioned for vessels fishing close to Puntarenas during trips of 2-3 d duration in 1980 when catches were poor.

The original 1974-79 effort data (Table 2) were adjusted to account for a presumed increase in the proportion of a 12-h day spent searching for fish as stock abundance declined and an improved capture efficiency associated with the construction of larger, more powerful vessels using larger nets. In the absence of reliable information on the decline in resource availability or increased vessel fishing power, the standardization procedures which were applied were very approximate, but served in some degree to counteract the probable underestimation of real fishing effort during the later years of the fishery as measured simply by the number of days at sea. The year 1974 was selected as the critical year to initiate effort standardization since it was in 1974 that the fleet, in response to declining yields in the Gulf of Nicoya, expanded operations in earnest to more distant fishing grounds (Table 4) and increased in size from five active vessels to seven. The fleet continued to exploit more distant fishing grounds during subsequent years and expanded to nine active vessels in 1975-77. Most of the larger vessels were first

TABLE 3.— Detailed catch and effort information recorded by observers aboard thread herring vessels fishing in the Gulf of Nicoya, Costa Rica, during August and September 1980. Source: Oficina de Pesca, Ministerio de Agricultura y Ganadería, Puntarenas, Costa Rica.

							Catch per unit effort			
Trip	Days ¹	Hours	H/d	Sets	Catch ² (t)	Search time (%)	t/d	t/h search	t/fishing h	t/total h
1	2	22.7	11.4	2	32.0	66	16.0	2.2	4.7	1.4
2	2	16.5	8.2	6	19.0	47	9.5	2.4	5.4	1.2
3	3	27.7	9.2	6	12.0	76	4.0	.6	2.9	.4
4	31	11.9	11.9	4	22.5	39	22.5	4.9	4.0	1.9
5	3	15.9	45.3	6	2.5	74	.8	.2	.8	.2
ÂII	11	94.7	8.6	24	88.0	63	8.0	1.5	3.8	.9

¹Calendar days absent from port.

²Estimated by captain.

³Two days were spent tuna fishing. ⁴Trip terminated early morning of day 3 due to equipment failure.

TABLE 4.— Distribution of reported 1968-79 fishing effort for thread herring among the three principal fishing zones on the Pacific coast of Costa Rica and percent of total effort expended in zones two and three. Source: Oficina de Pesca, Ministerio de Agricultura y Ganadería, Puntarenas, Costa Rica.

	Eff	ort (d at s	ea)		
Year	Zone 1	Zone 2	Zone 3	% total effort in zones 2-31	
1968	130	0	0	0.0	
1969	200	0	0	0.0	
1970	154	110	0	41,7	
1971	217	0	0	0.0	
1972	351	45	35	18.6	
1973	458	8	35	8.6	
1974	584	64	187	29.7	
1975	490	344	451	61.0	
1976	628	359	334	51.3	
1977	622	251	270	44.3	
1978	339	188	349	60.7	
1979	371	125	255	50.5	

¹Total effort includes a small amount of fishing in zone 4 which is not shown in this table.

registered in 1973 or later (Table 5). At least one of the newer vessels was equipped with directional sonar equipment, an addition which greatly aids in the location of schools.

TABLE 5.— Characteristics of purse seine vessels and gear which constituted the Costa Rican thread herring fleet in 1979. Vessels are ranked according to net tonnage and fall roughly into two groups according to size, horsepower, and the size of the net used by each vessel. Source: Oficina de Pesca, Ministerio de Agricultura y Ganadería, Puntarenas, Costa Rica.

Vessel	Year registered	Net tonnage (t)	Length (m)	Capacity (t)	Horse- power	Net size (m)
			Group 1			
1	1975	20	13.7		150	
2	1971	30	15.2	27	180	324 × 32
3	1971	33	17.1	33	125	324 × 32
4	1973	35	17.7	30	180	324×32
5	1971	40	15.2	38	40	324 × 32
¹ 6	1973	40	18.9	45	228	360×45
			Group 2	2		
7	1973	42	24.4	60	500	450 × 36
8	1973	51	24.4	70	420	450 × 36
9	1973	56	26.5	120	360	504 × 36
10	1977	70	22.9	70	240	
11	1975	75	22.9	60	330	486×54

'This vessel was lost at sea in October 1979.

Original 1974-79 effort data were adjusted (Table 6) to account for increased search time by increasing observed effort in five 5% annual increments beginning in 1975 and by a constant 25% annual increment to account for increased fishing power beginning in 1974. The first adjustment was based on the presumption that no more than 5 h in an average 12-h day (or 50% of the total fishing time after deducting 2 h for travel to and from port) were spent searching for fish in the early years of the fishery when fishing was concentrated primarily in the Gulf of Nicoya (Table 4), whereas 9 out of 12 h (75%) may have been spent searching for fish in 1979, assuming that the fish were less abundant and that vessels which travelled longer distances to and from fishing grounds in zones two and three devoted most of their daylight transit time to searching. This last assumption has in fact been confirmed by vessel captains. Observations made aboard vessels fishing near Puntarenas in 1980 during only 11 d (Table 3) showed that 63% of the daylight hours were devoted to searching. Since catch data originally collected for individual vessels and trips were no longer available when this assessment was conducted, the relative fishing power of individual vessels and the factors affecting vessel performance could not be determined.

Yield Analyses

Maximum equilibrium yield (Y_s) and its corresponding effort (f_s) were estimated by applying the linear and exponential forms of the surplus production model to annual catch and effort data compiled during 1969-79. These data were collected beginning in 1968 when fishing began and represented fishing activity during an initial period of high CPUE and low effort, an intermediate period when larger vessels were built and

TABLE 6.—Annual 1974-79 catch, adjusted effort and adjusted catch per unit effort (CPUE) statistics for three species of thread herring captured on the Pacific coast of Costa Rica. Original effort data were adjusted to account for a presumed 25% annual increase in vessel fishing power beginning in 1974 and an additional 5% annual increment to account for a presumed increase in search time per day at sea beginning in 1975.

Year	Catch Ct (1)	Original effort ft (d at sea)	Correction factor	Adjusted effort <i>xtft</i> (standard d)	Adjusted CPUE Ct/xtft (t/standard d)	Average effort $\frac{1}{2}(x_t f_t + x_t - 1f_t - 1)$ (standard d)
1974	7,193	844	1.25	11,055	6.82	778
1975	7,592	1,304	1.30	1,695	4.48	1.375
1976	6,330	1,350	1.35	1,822	3.47	1,758
1977	6,619	1,176	1.40	1,646	4.02	1,734
1978	5.034	884	1.45	1,282	3.93	1 464
1979	4,654	753	1.50	1,130	4.12	1,206

¹xtft in 1973 was 1.0(501 d) = 501 d.

the fleet expanded to new fishing grounds in response to declining CPUE and a later period characterized by diminished total production and severely reduced CPUE throughout the entire geographic range of the fishery. Estimates of maximum equilibrium yield and the amount of fishing effort required to produce that yield could serve as "starting points" for management strategies intended to conserve the Costa Rican thread herring resource and achieve maximum social and economic benefits from the fishery.

The linear surplus production model was first outlined by Graham (1935) and further developed by Schaefer (1954). These authors postulated that under equilibrium conditions the instantaneous rate of surplus production from a given population at any time (t) is directly proportional to the biomass (B_t) of the population at that time and to the difference between the theoretical maximum biomass (B_x) and B_t and inversely proportional to B_{xy} , i.e.

$$\frac{dB}{dt} = \frac{kB_t(B_{\infty} - B_t)}{B_{\infty}} \tag{1}$$

where k = the instantaneous rate of increase in stock size at densities approaching zero.

Moreover, when the biomass which exceeds an equilibrium level (B_E) is being removed at the same rate as it is produced, the surplus production (dB/dt) is converted into an annual equilibrium yield (Y_E) according to the following expression:

$$\frac{dB}{dt} = Y_E = F_E B_E \tag{2}$$

where F_E = rate of fishing which maintains the population at B_E .

If we assume that the rate of fishing (or instantaneous rate of fishing mortality) at equilibrium is proportional to the fishing intensity (or effort) then

$$F_E = q f_E \tag{3}$$

where f_E = fishing effort under equilibrium con-

ditions

q = the coefficient of "catchability," i.e., the vulnerability of the population to fishing.

From Equations (1) and (2), at equilibrium

$$\frac{dB}{dt} = Y_E = F_E B_E = \frac{k B_E (B_{\infty} - B_E)}{B_{\infty}}.$$
 (4)

Substituting Y_E/F_E for B_E in Equation (4)

$$Y_E B_E = F_E B_{\infty} - \frac{B_{\infty}}{h} F_E^2$$
 (5)

and from Equation (3)

$$Y_E = q B_{\infty} f_E - \frac{q^2 B_{\infty}}{k} f_E^2$$
 (6)

which defines a parabola in which Y_E is a function of f_E .

Dividing both sides of Equation (6) by f_E yields a linear relationship $Y_E/f_E = a + bf_E$ where the intercept $a = qB_{\infty}$ and the slope $b = q^2B_{\infty}/k$. The effort f_s which corresponds to the maximum equilibrium catch Y_s is determined from the relationship

$$\frac{dY_E}{df_E} = a - 2bf_E = 0.$$
(7)

Therefore

$$f_E - f_s = \frac{a}{2b} . \tag{8}$$

Substituting Equation (8) in Equation (6), the maximum equilibrium yield Y_s determined from the regression function is

$$Y_E = Y_s = \frac{a^2}{4b}.$$
 (9)

Thus, when Equation (3) is valid, estimates of maximum equilibrium yield and associated effort

can be obtained from CPUE and effort data compiled from a unit stock fishery under equilibrium conditions even when the catchability coefficient (q) is unknown.

Since catch and CPUE will usually be related to effort within a single year and during several preceding years, Gulland (1969) has argued that the abundance of a particular year class which has been in the fishery for x years would be influenced by the fishing mortalities during those x years and proposed that the total CPUE for all ages during any given year would be related to some weighted mean of fishing effort in those x years. According to Gulland (1969), if this mean is taken over a period of time equal to the mean duration of life in the exploited phase, then the relation between CPUE and this mean effort \overline{f} will approximate that between CPUE and effort in the steady state.

An exponential form of the surplus production model was developed by Fox (1970) to express the nonlinear relationship between CPUE and effort statistics. The exponential surplus production model was based on the assumption that the rate of population increase was best described by the Gompertz growth function rather than the logistic growth function assumed by the linear form of the model. For the exponential model, under equilibrium conditions

$$\frac{dB}{dl} = kB_E(\log_e B_\infty - \log_e B_E)$$
(10)

and the annual equilibrium yield (Y_E) is therefore

$$\frac{dB}{dt} = Y_E = kB_E(\log_e B_\infty - \log_e B_E).$$
(11)

Since CPUE (Y/f = U) is defined to be proportional to population biomass

$$B_E = \frac{1}{q} \left(\frac{Y_E}{f_E} \right) = \frac{U_E}{q} , \qquad (12)$$

Equation (11) can be rewritten as

$$\frac{dB}{dt} = Y_E = \frac{U_E}{q} k \left(\log_e \frac{U_{\infty}}{q} - \log_e \frac{U_E}{q} \right). \quad (13)$$

Collecting terms and dividing through by U_E (= Y_E/f_E)

$$f_E = \frac{k}{q} \left(\log_e U_{\infty} - \log_e U_E \right)$$
(14)

or

$$\log_e U_E = \log_e U_{\infty} - \left(\frac{q}{k}\right) f_E \tag{15}$$

which is equivalent to

$$U_E = U_{\infty} e^{-bf_E} . \tag{16}$$

Multiplying Equation (16) by the fishing effort at equilibrium (f_E)

$$Y_E = f_E U_{\infty} e^{-bf_E} \,. \tag{17}$$

Therefore, the effort (f_s) which produces maximum equilibrium yield (Y_s) is determined from the relationship

$$\frac{dY_E}{df_E} = -bf_E U_{\infty} e^{-bf_E} + U_{\infty} e^{-bf_E} = 0 \quad (18)$$

and

$$f_s = \frac{1}{b} . \tag{19}$$

Since $bf_s = 1$, CPUE at $f_s(U_s)$ is

$$U_s = U_{\infty} e^{-bf_s} = \frac{U_{\infty}}{e}$$
(20)

and the maximum equilibrium yield (Y_s) is given by

$$Y_s = f_s U_s = \frac{U_\infty}{be}.$$
 (21)

696

 Y_s and f_s were estimated from linear and exponential regressions of CPUE vs. effort when the effort corresponding to a given year's catch was set equal to effort applied during the same year (f_t) , or an average of the effort applied buring the same year and the previous year (\overline{f}) . For the purposes of calculating average effort, it was assumed that thread herring exploited in Costa Rican waters were recruited to the fishery at age 1 and remained in the exploitable size range for 3 yr. Effort was therefore averaged for a 2-yr period according to the procedure described by Gulland (1969) on the presumption that the mean duration of life in the exploitable size range was 2 yr. This assumption was generally supported by age and growth observations for species of this genus (Houde 1976: Sokolov and Wong footnote 5; Paez Barrera footnote 3; Reintjes footnote 4) but needs to be confirmed by specific growth studies.

A total of eight pairs of Y_s and f_s estimates were obtained from both the original and standardized data sets (Table 7). Analysis of the variance due to random error after regression was evaluated by calculating F-statistics. All regressions were performed for 1969-79 data since the 1968 catch was extremely low relative to the amount of effort expended (Table 3), suggesting that the single vessel which was in operation that year was not performing to its full capacity. For each model, predicted yield values for f_E = average observed effort and f_E = average standardized effort were plotted and compared with actual annual 1969-79 yields. Values of equilibrium yield (Y_E) predicted by each model for given values of equilibrium effort (f_E) were calculated according to

$$Y_E = af_E - bf_E^2$$
 (22)

for the linear model, and

$$Y_E = af_E e^{-bf_E}$$
(23)

for the exponential model.

RESULTS AND DISCUSSION

The results (Table 7) indicated a range of Y_s and f_s estimates depending on the model, the form of the independent variable (f_t or \overline{f}), and whether or not effort was standardized. For all cases, Y_s ranged from 6,290 to 7,890 t. A wider range of Y_s estimates was predicted by the linear model (6,700-7,890 t) as compared with the exponential model (6,290-6,730 t). Observed f_s estimates ranged from 888 to 1,067 d and standardized f_s estimates ranged from 1,041 to 1,117 standard days. Given the range of options which were tested, these ranges were not extreme. All regressions were statistically significant at >99% confidence levels.

Based on the "goodness of fit" as evaluated by the *F*-statistic, \overline{f} produced a better fit than f_t in all cases, as did the exponential model as opposed to the linear model and the standardization of effort. The improved fit of the exponential model to CPUE vs. average observed and average standardized effort graphically was quite obvious (Figures 5, 6). Examining the independent effects on maximum equilibrium yield estimates produced by the standardization of effort data and the use of two different models, it was apparent that within each model standardization of the 1974-79 data increased Y_s , especially in the case of the linear model whereas use of the exponential model decreased Y_s estimates for both the standardized and observed data, but more significantly with the standardized data. Furthermore, the choice of f_t or \bar{f} as the independent variable had very little effect on the magnitude of these changes. Looking at the

TABLE 7.—Summary of maximum equilibrium yield (Y_s) , the amount of fishing effort which produces maximum equilibrium yield (f_s) , and Y_s/f_s estimates for the Costa Rican thread herring fishery as derived from linear and exponential surplus production models applied to 1969-79 catch per unit effort and effort data. Linear and exponential regressions were repeated using effort data collected during the same year (f_t) and average effort over a 2-yr period (\overline{f}) as well as observed and adjusted effort estimates (see Tables 2, 6). Analyses of variance (*F*-tests) indicated that all regressions were statistically significant at 99% confidence levels.

Model	Effort	Y-intercept a	Slope $\times 10^3$ b	Y _S ¹ (t)	f _S (d at sea)	Y _S /f _S (t/d)	F-statistic
Linear	fr observed	15.21	-8.317	6,950	914	7.60	41.4
	7 observed	15.09	-8,494	6,700	888	7.54	61.5
	ft adjusted	14.81	-6.952	7,890	² 1,065	² 7.41	58.4
	7 adjusted	14.51	-6.969	7,550	² 1,041	² 7.25	64.8
Exponential	ft observed	16.61	937	6,520	1,067	6.11	54.2
	/ observed	16.50	965	6,290	1,036	6.07	114.7
	ft adjusted	16.39	895	6,730	² 1,117	² 6.02	79.2
-	7 adjusted	15.96	912	6,430	²1,096	² 5.87	138.8

Rounded off to the nearest 10 t.

²Effort expressed in standard days at sea.



FIGURE 5.—Linear and exponential regressions of annual 1969-79 catch per unit effort versus observed effort averaged over a 2-yr period for three species of thread herring captured on the Pacific coast of Costa Rica.



FIGURE 6.—Linear and exponential regressions of annual 1969-79 catch per unit effort versus standardized effort averaged over a 2-yr period for three species of thread herring captured on the Pacific coast of Costa Rica. Effort was standardized to account for improved capture efficiency and reduced resource availability after 1973 (see text).

effects on effort at Y_s , the exponential model produced higher f_s estimates, but only significantly with observed effort data.

Using "goodness of fit" as the only criterion, the most acceptable Y_s estimate was 6,430 t. This Y_s was surpassed by 760 t in 1974 and by 1,160 t in

1975. Catch remained at this maximum equilibrium level in 1976 and 1977, but declined to the pre-1974 level in 1978 and 1979. In fact, all the yield analyses except the linear model as applied to standardized CPUE and effort data indicated overfishing in 1974 and 1975.

According to the "best" unadjusted f_s estimate (1,036 d), fishing effort in 1975 abruptly exceeded — by 20% — the level which produced the maximum equilibrium catch and remained excessive in 1976 and 1977. Observed effort declined dramatically after 1977. Using standardized effort as a guide, the most acceptable f_s estimate (1,096) standard days) was exceeded by an average annual amount of 57% during 1975-77. Assuming that the standardization procedure was accurate, "real" effort remained slightly above 1,100 standard days in 1978 and 1979 even though catches were considerably below the estimated Y_s of 6,430 t. The exponential model predicted that the maximum equilibrium vield would be maintained when CPUE was 6.1 t/d or 5.9-6.0 t/standard day. The linear model predicted considerably higher Y_s/f_s values.

A comparison of the predicted yield curves for both models—as applied only to average observed and standardized effort—with actual 1969-79 catches (Figures 7, 8) revealed a closer overall agreement between catch and predicted yields for the exponential model even though the linear model produced a closer agreement for certain



FIGURE 7.—Costa Rican thread herring yield curve predicted by the exponential and linear surplus production models and annual 1968-79 catch and average observed effort data.



FIGURE 8.—Costa Rican thread herring yield curves predicted by the exponential and linear surplus production models and annual 1968-79 catch and average standardized effort data.

years. Catches in 1972, 1974, and 1975 were considerably greater than Y_E values estimated by the exponential model. The linear model predicted actual yields more accurately through 1975, especially when effort data were standardized, but deviated substantially in 1976 and 1977.

The general tendency toward increasing effort ceased in 1978 and 1979 when substantially lower catches were taken with less effort (Figures 7, 8). Linear and exponential models were fit to 1969-77 data, using average effort only, since it appeared that a closer agreement between observed and predicted yields might be obtained if data for the last 2 yr were eliminated. This was not the case. Y_s estimates increased by 280-360 t and f_s estimates by about 50 d (Table 8), corresponding to a slight

TABLE 8.— Estimates of maximum equilibrium yield (Y_s) , the corresponding amount of fishing effort (f_s) and Y_s/f_s estimates for the Costa Rican thread herring fishery as derived from linear and exponential surplus production models for 1969-76. Only average observed and adjusted effort data were used.

The second se					
Model	Effort	Ys ¹ (t)	f _s (d at sea)	Y _S /f _S (t/d)	F- statistic
Linear	Observed	7.050	930	7.58	54.7
	Adjusted	7.910	² 1.090	7.26	49.1
Exponential	Observed	6.570	1.075	6.11	124.8
	Adjusted	6,780	²1,149	5.90	138.2

¹Rounded off to the nearest 10 t.

²Effort expressed in standard days at sea.

shift upwards and to the right in the predicted yield curves, but no statistical improvement in fit could be demonstrated. Yield analyses therefore were quite robust since approximately the same results were obtained from the two data sets.

Evaluation of the Model

A fundamental assumption of the surplus production yield model is that surplus population growth that is harvested by the fishery is at any point in time a function of population biomass. Under the assumption that fishing mortality is directly related to fishing effort by a constant proportionality factor, changes in the rate of population growth can also be related to fishing effort. Thus, the model assumes equilibrium conditions, i.e., that changes in population size -- as estimated by CPUE—will remain in equilibrium with a given fishing effort. For developing fisheries in which effort is continually increasing, this equilibrium seldom has an opportunity to become established. Even in cases where effort does stabilize, variations in population size (and therefore, yields) can be expected, especially if recruitment is highly variable and bears little relation to spawning stock size. The problem is further exacerbated if there is a significant delay between spawning and recruitment since the model assumes that the response of equilibrium vield to changes in population size is immediate. In fact, vield in any given year will seldom be related to population size during the same year.

For the Pacific thread herring, the presumed lag time between spawning and recruitment was small (1 yr?) and correction procedures were not employed. The relationship between recruitment and stock size for *Opisthonema* spp. was not known, but the fact that the Costa Rican thread herring population declined without major interruptions once the fishery began suggests that recruitment fluctuations were not extreme. If recruitment had varied significantly as stock size declined, the reduction in CPUE with increasing effort (Figures 5, 6) would not have been so uniform and the model would not have fit the data nearly so well.

A major problem which is common to all surplus production yield analyses is the nonindependence of X and Y variables when CPUE is plotted as a function of effort. As pointed out by Sissenwine (1978), the relationship between X and its reciprocal is hyperbolic. Therefore, CPUE vs. effort relationships are inherently biased. Following Gulland's (1969) procedure for averaging effort in the independent variable, not only does the model

more closely approximate equilibrium conditions, but the replacement of f_t by \overline{f} reduces the interdependence of the two variables. However, as demonstrated by Roff and Fairbairn (1980), temporal trends in effort such as those observed for the Costa Rican thread herring fishery produce correlations between f_t and \overline{f} since both are increasing (or decreasing). This autocorrelation in the independent variable in turn indicates a spurious correlation between CPUE and average effort. In the examples examined by those authors, the degree of autocorrelation between f_t and \overline{f} increased when shorter time periods were used to calculate \overline{f} . Furthermore, for periods of 2 or 3 yr, there was a significant correlation between f_t and \overline{f} even in the absence of trends in f_t over time.

In the present assessment, since there were definite trends in both standardized and unstandardized effort and since effort was averaged over only a 2-yr period, the nonindependence of the variables in the regression analyses could not have been significantly reduced. In fact, an examination of the deviations between observed and predicted CPUE for both models as applied to average observed and standardized effort (Figure 9) revealed considerable time trends. These trends were more obvious after effort standardization. Clearly, the variables in the regression analyses were not independent. Strictly speaking, therefore, the F-test used to evaluate the degree of fit was not valid since it assumes that Y observations are independent and normally distributed with common variance. Residual mean squares for the individual regression analyses, however, assume nothing about the distributive properties of the error term in the regression model. Although they cannot be used to evaluate the statistical significance of fit, they did confirm that better fits were obtained with average effort, the exponential model and standardized effort.

A second problem which was not addressed was the assumption that fishing mortality remained directly proportional to fishing effort (Equation (3)) as population size diminished. Thread herring may remain vulnerable to capture even at low stock sizes since they congregate in schools at the surface, i.e., the same fishing mortality may be exerted even with reduced effort. If fishing mortality and effort do not remain directly proportional, the surplus production model is not appropriate for predicting maximum equilibrium yields. There was no way to evaluate this possible source of error.



FIGURE 9.—Residual (observed-predicted) 1969-79 catch per unit effort values for the linear and exponential yield models arranged in chronological sequence.

Despite these problems, the surplus production model provided a clear analytical interpretation of the data. The range of Y_s and f_s estimates was not extreme, although the linear model applied to standardized data produced higher Y_s estimates than the other analyses. While there was no basis for assessing how "correct" the standardization procedure was, it did result in higher Y_s and f_s estimates for both the linear and exponential models and improved the least squares fit to the data, especially for the exponential model. Clearly, some adjustment in observed effort was called for. Acceptable estimates of Y_s and f_s were obtained from a fairly short time series of catch and effort data (11 yr). The success of this assessment was due in part to the reliability of the catch and effort data provided by the canning companies to the Ministry of Agriculture, and the fact that data

were available from the beginning of the fishery as well as from the period characterized by diminishing yields.

Management Implications

This assessment of the Costa Rican thread herring resource indicated that a maximum equilibrium yield of approximately 6,430 t was surpassed in 1974-75, leading to stock depletion and reduced catches in subsequent years. Declining catches during 1976-79 were certainly due only in part to reduced effort. Effort increased dramatically after 1973 and remained in excess of f_s (1,036 d) during 1975-77. "Real" effort may have remained slightly above optimum even in 1978 and 1979 when catch declined to about 5,000 t.

Management thus far has been self imposed by the industry in response to rapidly declining CPUE. Economic returns have presumably suffered at least as much as biomass yields. To protect the resource. Costa Rican Government regulation would only be necessary if effort again approached 1,000 d at sea or if catch exceeded 6,500 t. Regulation of effort should concentrate on "real" effort, not merely the number of days vessels spend at sea. It would be important, therefore, to maintain effort at some level below 1,000 d if fishing power were suddenly increased, say, by the use of aircraft to spot schools of fish. Since real effort is not easily measured, a catch quota might be a more practical management strategy. Given the small number of vessels in the fishery, allocation of vessel quotas would be feasible. A reduction in the number of vessels, however, would more effectively maintain acceptable economic returns for the industry. Maximum economic returns would presumably be achieved at some effort level below f_s .

Once an exploited population is depleted, biomass can be restored to a level which supports maximum equilibrium yield by reducing the harvest of adults, thus reducing adult mortality and stimulating increased recruitment. Catch should be maintained at reduced levels for a period of time equal to the delay between spawning and recruitment. As a general policy, fishing at below Y_s also protects to some extent against additional stock depletion due to poor recruitment. For the Costa Rican thread herring population, some increase in stock size (and therefore CPUE) following overfishing in 1974-75 should have been noticeable after a year or two of reduced catches such as occurred in 1978-79. The observed increase in CPUE since 1976 (Table 2, Figure 2) was small and may not have been "real" since standardized CPUE stabilized after 1976 (Table 6). However, catch and effort data available for the first 5 mo of 1980 (Table 9) showed a continued low CPUE when compared with the same period in 1979.

TABLE 9.—Observed catch, effort, and CPUE data compiled from sales receipts for the first 5 mo of 1979 and 1980 for thread herring captured on the Pacific coast of Costa Rica. Source: Oficina de Pesca, Ministerio de Agricultura y Ganadería, Puntarenas, Costa Rica.

Period	Catch (t)	Effort (d at sea)	CPUE (t/d at sea)
JanMay 1979	2,270	330	6.88
Jan May 1980	1,860	340	5.47

Unit stock identification is an important area requiring further research. Although thread herring on the Pacific coast of Central America may not be highly migratory, it seems likely that there is some mixing across national boundaries. The rapid decline in population size in Costa Rican waters—as inferred from reduced CPUE estimates-would not have been possible, however, if there had been a significant influx of fish from other areas along the Central American coastline. The Panamanian thread herring fishery is only active in the Gulf of Panama, although thread herring were detected acoustically in the Gulf of Chiriqui (see Figure 1) and off Guatemala, El Salvador, and Nicaragua during a 1970 survey (Magnusson 1971). If the same stock is presently being exploited in Costa Rican and Panamanian waters, stock assessment and resource management should be a joint activity of both countries. The possibility also exists that more than one stock is present in Costa Rican waters, either geographically or taxonomically. Clearly, the assumption that the three species which currently make up the catch can be treated as a single unit stock needs to be confirmed with additional ecological and life history information. In the meantime, efforts should be made to determine the species composition of landings, and to compile catch and effort data by species.

SUMMARY

1. Catch and effort data were compiled for three species of Pacific thread herring harvested in Costa Rican waters during 1968-79. Effort was estimated as the number of calendar days at sea. Data were available from the beginning of the fishery and from a period of diminishing and declining yields.

2. Effort data were standardized to account for a presumed 25% increase in capture efficiency beginning in 1974 when larger, more powerful vessels with larger nets first entered the fishery and for a presumed 5% annual increment in the proportion of time spent searching for fish as stock size declined beginning in 1975.

3. Estimates of maximum equilibrium yield (Y_s) were obtained by fitting linear and exponential forms of the surplus production model to plots of catch per unit effort (CPUE) vs. effort. Eight yield analyses were performed using observed and standardized effort to calculate CPUE and a moving 2-yr average of observed and standardized effort as well as simple annual observed and standardized effort as the independent variable.

4. All regression analyses were statistically significant at the 99% confidence level. The standardization and averaging of effort data, and the use of the exponential model improved the degree of statistical fit. The predicted yield curves fit observed catch data fairly well.

5. Y_s estimates ranged from 6,290 to 7,890 t, observed f_s ranged from 888 to 1,067 d and standardized f_s ranged from 1,041 to 1,117 standard days. The best fit to the data was obtained with the exponential model applied to standardized CPUE vs. average standardized effort data. This analysis produced a Y_s estimate of 6,430 t and a f_s estimate of 1,096 standard days. The best estimate of unstandardized effort was 1,036 d.

6. The "best" Y_s estimate was exceeded by 760 t in 1974 and by 1,160 t in 1975. Overfishing probably contributed to catches of 5,000 t and lower in 1978-79. Observed effort abruptly exceeded f_s in 1975 by 20%, remained above 1,000 d in 1976 and 1977, and then declined dramatically in 1978-79. Standardized effort remained slightly above standardized f_s even in 1978 and 1979.

7. Attempts to reduce the dependence of the CPUE and effort variables in the regression analyses by averaging effort were of doubtful value since there was a trend toward increasing effort as the fishery developed and since only 2 yr were used to average effort. Thus, significant autocorrelations between f_s and \overline{f} could not be avoided. Obvious time trends in the deviations between predicted and observed CPUE provided evidence for the nonindependence of the variables in the regression analyses. This problem, however,

was not believed to have seriously altered the results of the assessment.

8. The industry should be encouraged to either maintain effort below 1,000 d at sea or annual catch below 6,500 t as was done in 1978 and 1979. If regulations are necessary, a catch quota may prove to be more feasible since it could fairly easily be allocated to individual vessels and since effort limitations must consider "real" changes in fishing effort which are difficult to quantify. On the other hand, a reduction in the number of vessels would improve economic returns for the fishing vessels which remain in the fishery.

9. Unit stock identification is an important area requiring further research. The inferred rapid reduction in stock abundance in Costa Rican waters suggests that there was little net immigration of thread herring from neighboring countries, but the degree to which the stock (or stocks) exploited by the Costa Rican fleet may also be exploited elsewhere (Panama, in particular) needs to be clarified.

ACKNOWLEDGMENTS

The authors wish to thank the vessel captains and the owners and managers of the three Costa Rican canning companies for their cooperation; the biologists, assistant biologists, and statisticians of the Ministry of Agriculture Fisheries Office in Puntarenas, Costa Rica, for compiling catch and effort data; and to Eduardo Bravo, Milton Lopez, and Eduardo Lopez of the Ministry of Agriculture Fisheries Resources and Wildlife Division, San Jose, Costa Rica, for their encouragement and support. Thanks are also extended to Adan Chacon of the Costa Rican Ministry of Agriculture and David Sampson of the Maine Department of Marine Resources for their assistance with mathematical and statistical procedures and to four anonymous reviewers for their constructive criticism.

LITERATURE CITED

BERRY, F. H., AND I. BARRETT.

1963. Gillraker analysis and speciation in the thread herring genus *Opisthonema*. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Bull. 7:111-190.

BEVERTON, R. J. H.

1963. Maturation, growth and mortality of clupeid and engraulid stocks in relation to fishing. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer 154:44-67. FOOD AND AGRICULTURE ORGANIZATION.

1979. Catches and landings, 1978. FAO, Yearb. Fish. Stat. 46, 372 p.

FOX, W. W., JR.

1970. An exponential surplus-yield model for optimizing exploited fish populations. Trans. Am. Fish. Soc. 99.80-88

FUSS, C. M., JR., J. A. KELLY, JR., AND K. W. PREST, JR.

1969. Gulf thread herring: aspects of the developing fishery and biological research. Proc. Gulf Caribb. Fish. Inst. 21:111-125.

GRAHAM. M.

1935. Modern theory of exploiting a fishery, and application to North Sea trawling. J. Cons. 10:264-274. GULLAND, J. A.

1969. Manual of methods for fish stock assessment. Part 1. Fish population analysis. FAO Man. Fish. Sci. 4, 154 p. HOUDE, E. D.

1976. Abundance and potential for fisheries development of some sardine-like fishes in the eastern Gulf of Mexico. Proc. Gulf Caribb. Fish. Inst. 28:73-82.

KINNEAR, B. S., AND C. M. FUSS, JR.

1971. Thread herring distribution off Florida's west coast. Commer. Fish. Rev. 33(7-8):27-39.

KLIMA, E. F.

1971. Distribution of some coastal pelagic fishes in the western Atlantic. Commer. Fish. Rev. 33(6):21-34.

MAGNUSSON, J.

- 1971. Pacific coast pelagic survey off Central America and Panama Bay, June 1970-January 1971. Proj. Reg. Desarr. Pesq. Centro-Am. Bol. Tec. IV(6), 32 p.
- MURPHY, G. I.
 - 1977. Characteristics of clupeoids. In J. A. Gulland (editor), Fish population dynamics, p. 283-308. Wiley, N.Y.

PETERSON, C. L.

1956. Observations on the taxonomy, biology and ecology of the engraulid and clupeid fishes in the Gulf of Nicoya, Costa Rica. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Bull. 1:137-280.

PRISTAS, P. J., AND R. P. CHEEK.

1973. Atlantic thread herring (Opisthonema oglinum) movements and population size inferred from tag returns. Fish. Bull., U. S. 71:297-301.

ROFF, D. A., AND D. J. FAIRBAIRN.

1980. An evaluation of Gulland's method for fitting the Schaefer model. Can. J. Fish. Aquat. Sci. 37:1229-1235. SCHAEFER, M. B.

1954. Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. Inter-Am. Trop. Tuna Comm., Bull. 1:25-56.

SISSENWINE, M. P.

1978. Is MSY an adequate foundation for optimum yield? Fisheries 3(6):22-24, 37-38, 40-42.