CHANGES IN SIZE OF THREE DOLPHIN (*STENELLA* SPP.) POPULATIONS IN THE EASTERN TROPICAL PACIFIC

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ABSTRACT

Dolphins from three populations, one of *Stenella attenuata* and two of *S. longirostris*, have been killed incidentally in the yellowfin tuna purse seine fishery in the eastern tropical Pacific, two populations since about 1959 and the other since about 1969. Size changes in these populations are estimated from numbers killed each year, population size estimates in 1979, and net recruitment rates. Ranges of values for some parameters are considered, accounting for some uncertainties. Assuming central values of the ranges of maximum net recruitment rate (3%) and the population level giving maximum net productivity (65%), one *S. longirostris* population, the eastern spinner dolphin, is near 20% of pre-exploitation levels; the *S. attenuata* population, the northern offshore spotted dolphin, is between 35 and 50%; and the second *S. longirostris* population, the whitebelly spinner dolphin, is between 58 and 72% of pre-exploitation levels.

Purse seine fishing for tuna in the eastern tropical Pacific often involves dolphins found in association with yellowfin tuna. Tuna fishermen pursue and capture the dolphin-yellowfin tuna complex, releasing the dolphins from the net while retaining the tuna (Green et al. 1971). Mortality of dolphins occurs incidental to this fishing process.

Purse seine fishermen were using dolphin schools to catch tuna by 1959; there is anecdotal information suggesting limited use as early as the 1940's (anonymous reviewer). Starting in the mid-1960's the Bureau of Commercial Fisheries, predecessor of the National Marine Fisheries Service (NMFS), conducted limited research to document the situation and to collect data on numbers and kinds of dolphins killed. This research expanded in the 1970's, especially after passage of the Marine Mammal Protection Act (MMPA) of the United States in 1972, and continues. Substantial research efforts were mounted to assess the status of the dolphin stocks and to develop procedures for reducing incidental mortality and injury.

Two assessments of the condition of dolphin populations involved in the yellowfin tuna purse seine fishery have been completed in recent years.[2,3] I describe the results of the latest assessment of the three populations most affected by the fishery; calculation of population sizes from 1959 through 1978 is emphasized, based on estimates of the population size in 1979, on annual numbers killed from 1959 through 1978, and on net recruitment rates. These results, based on data available through the end of 1980, do not necessarily represent NMFS policy, which involves additional considerations. A third assessment of these populations is scheduled for 1984 and will include information since 1980.

POPULATION MODEL

Methods developed in 1976 (footnote 2) for estimating pre-exploitation abundance are based on a simple recursive relationship

$$N_{t+1} = N_t - K_t + R_t (N_t - \tfrac{1}{2} K_t),$$

where t denotes the year; N, the abundance; K, the number of animals killed; and R, the net recruitment rate. This model assumes that the population size in the next year is simply the present population size, minus the present incidental kill, plus the net number of individuals recruited to the population during the year. This latter quantity is taken to be the net recruitment

rate (birth rate less natural death rate) multiplied by the number of animals actually reproducing in a given year. The number of reproducing animals is approximated by assuming that one-half the animals killed in a year reproduce before dying. Solving this relationship for N_t, one obtains

$$N_t = \frac{N_{t+1} + \frac{1}{2} K_t}{1 + R_t} + \frac{1}{2} K_t. \qquad (1)$$

Repeatedly applying this equation to estimate the population size for any number of years (s) prior to the year (c) for which an independent estimate of population size (N_c) is available yields in general

$$N_s = \frac{N_c}{\prod_{i=1}^{s}\left(1 + R_i\right)} + \sum_{j=1}^{s} \frac{K_j\left(1 + \frac{1}{2} R_j\right)}{\prod_{i=j}^{s}\left(1 + R_i\right)}. \qquad (2)$$

The 1979 workshop (footnote 3) extended this procedure by calculating the recruitment rate R_i, i years prior to the present, using the density-dependent relationship (Allen 1981)

$$R_i = R_m \left\{ 1 - \left(\frac{N_i}{N_p}\right)^z \right\}. \qquad (3)$$

N_p is the estimated population size at the beginning of the first year of exploitation, p years earlier; R_m, the maximum net recruitment rate; Z, the density-dependent exponent; and N_i and N_p, estimated from Equation (2). Because N_p in Equation (3) is not known until the series in Equation (2) has been calculated, an iterative procedure is required to solve the equations for historical population size. Equations (1) and (3) together form a special case of the generalized production model of Pella and Tomlinson (1969).

In Equation (3) the net recruitment rate is maximum (R_m) when the population size approaches zero, decreasing to zero as the population size approaches N_p. Z determines the population size at which the rate of change of the population is maximum, the maximum net productivity level $(MNPL)$. The values of Z correspond to the $MNPL$ approximately as (Polacheck 1982)

$$MNPL = \frac{N_p}{\left(1 + Z\right)^{1/z}}. \qquad (4)$$

If $Z = 1$, then the $MNPL$ is one-half the equilibrium population size; if Z is >1, then $MNPL$ is greater than one-half the equilibrium size. The fraction of the maximum reproductive rate, R_m, realized at a given population size, increases as the value of Z increases.

Statistical properties of the estimate of N_p and the ratio N_c/N_p are examined in detail in Smith and Polacheck (1979), wherein methods are developed for calculating the variances. Tests of sensitivity of the estimates of N_p to the values N_c, K_t, and R_m show that the estimates are most sensitive to the value of present abundance and least sensitive to the net recruitment rate. Examination via simulation of the shape of the sampling distribution shows that if N has a symmetrical sampling distribution, then so does the estimate N_p.

Several estimates of each parameter required by the model are available in working documents and technical memoranda prepared by the staff of the Southwest Fisheries Center. I rely on the most current estimates, primarily minor revisions of those used by the 1979 workshop, with reference to papers describing earlier estimates as needed to document methods.

POPULATIONS

Populations affected most by the yellowfin tuna purse seine fishery are of the genus *Stenella*, and are found in the area from just south of the Equator to an approximate lat. 20°N and west from the Mexican and Central American coasts to an approximate long. 150°W. Two populations of spotted dolphins, *S. attenuata*, and three populations of spinner dolphins, *S. longirostris*, are found in this region.

The two spotted dolphin populations are referred to as "offshore" and "coastal" forms. The coastal spotted dolphin population occurs nearshore and around islands, while the offshore spotted dolphin ranges from nearshore to an approximate long. 150°W. The two forms overlap in range near the coast.

Perrin (1975) distinguished these two forms of *S. attenuata* morphologically. He noted that 1) the larger coastal form occurs seaward to 50 km while the offshore form occurs as nearshore as 20 km, and 2) the coastal form was involved in only 7 of 1,373 purse seine sets on dolphins observed between 1971 and 1974. Additional data collected since then, including reexamination of specimens collected during sets in the years 1971-74,

indicate that through 1978, a total of 22 sets have been observed on coastal spotted dolphins, out of a total 9,672 observed overall (about 0.2%).

The yellowfin tuna purse seine fishery was concentrated nearshore in the early 1960's, and many sets were made in the area probably occupied by both coastal and offshore spotted dolphins. Direct observations in the 1960's distinguishing these forms of the spotted dolphin are not available. Based on observations made in the 1970's where these forms were distinguished, however, it appears that the coastal form has never been significantly involved in this fishery. Since 1978, sighting data collected by scientific observers aboard tuna vessels have been edited, using consistent criteria of school size, body size, and coloration for distinguishing coastal and offshore spotted dolphins. In 1979, for example, within about 50 km of the coast there were 46 sightings of coastal spotted schools, 160 sightings of offshore spotted schools, and 25 sightings of spotted dolphin schools which could not be distinguished to form with the available data. These three school types were subsequently set on in 2, 73, and 6 instances, respectively. Even assuming that all schools not identified to form were coastal spotted dolphins, the proportion of sighted coastal spotted dolphin schools subsequently set on is much smaller than that of the offshore form (0.11 vs. 0.46, $P<0.001$). This differential selection exists even though the catch of yellowfin tuna in sets on coastal spotted dolphins has been approximately twice that on offshore spotted dolphins. If coastal spotted dolphins were a significant part of this fishery, one would expect their involvement in sets to be proportional to the rate at which they are encountered.

In addition, 18 of the 22 sets on coastal spotted dolphins occurred in 1973, and, except for one set, these were made by two vessels in the Gulf of Nicoya, a small area off the Costa Rican coast. Based on this information, I have assumed that the coastal spotted dolphin has been involved only rarely in this fishery.

Two spinner dolphin populations, referred to as the "eastern" and "whitebelly" forms, are involved in the yellowfin tuna purse seine fishery. A third form, termed the Costa Rican spinner, occurs near the coast from Mexico to Panama, but is not involved in the fishery. The eastern and whitebelly forms overlap broadly in range, with the whitebelly spinner dolphin generally occurring more seaward. The eastern form has been involved with this fishery since 1959, whereas the whitebelly spinner dolphin population apparently became increasingly involved as the fishery expanded seaward in the 1960's.

The whitebelly spinner and the offshore spotted forms have Southern Hemisphere populations (Perrin et al. 1979). These populations have been involved only recently with the yellowfin tuna purse seine fishery, as it has expanded southward, and are only lightly exploited. Data on reproductive condition of these southern populations are used as estimates of reproductive rates for unexploited or equilibrium populations.

1979 POPULATION SIZE ESTIMATES

Holt and Powers (1982) gave estimates of abundance based on aerial and research-vessel sighting surveys and data from scientific observers aboard fishing vessels. Estimates of the size, N_i, of the ith population in their survey area are based on the equation

$$N_i = P_t \, S_t \, D \, P_i \, A, \qquad (5)$$

where P_t denotes the proportion of dolphin schools containing dolphin of the genera *Stenella*, *Delphinus*, and *Lagenodelphis*; S_t, the mean size of these schools; D, the estimated density of all dolphin schools sighted; P_i, the fraction of schools containing dolphins of the ith population; and A, the area inhabited. This equation is applied to 1) a nearshore stratum, surveyed using both an airplane and research vessels, and 2) an offshore stratum, surveyed only by research vessels. The nearshore stratum extends seaward from the coastline about 800 km, and from lat. 22°N to 12°S. The offshore stratum extends from the outer edge of the nearshore stratum to the boundary of the dolphin range.

Approximate areas of the maximum historical range of the three dolphin populations are used for the area inhabited, A in Equation (5). These are estimates of the area enclosed by a smooth curve which includes most locations where dolphins of different species have been reported by both fishing vessels and research vessels, as described in Holt and Powers (1982).

While occasional sightings of dolphin schools have been reported outside these areas, the areas are overestimated in that "...at any point in time it is likely that each of the various dolphin species

only occupies a portion of its historical range."[4] Overlap between coastal and offshore forms of spotted dolphin is not reflected in the population estimates given by Holt and Powers (1982). Due to the large differences in areas inhabited, however, adjustments to account for the unknown degree of overlap would increase the offshore spotted dolphin population estimate by 3% at most, which is insignificant for the general results being presented here.

The density estimate for the nearshore area is obtained from line transect theory applied to aerial survey sighting data. This follows earlier applications (Smith 1981), but with several improvements. For instance, the aircraft we used had superior downward visibility; right-angle distance from the aircraft trackline to the sighted dolphin schools was determined directly, either by electronic navigation equipment or visually for shorter distances, rather than being calculated from visual estimates of range and bearing; and the originally used negative-exponential sighting model was replaced with the superior Fourier series model (Burnham et al. 1980). The density estimate for the offshore area, which could not be surveyed by air, is obtained by comparing relative dolphin school sighting rates from research vessel surveys in nearshore and offshore areas with absolute density estimates from the nearshore area. The resulting density estimate of all dolphin schools of >15 animals in the nearshore area is about 3.6 schools/1,000 km^2, while the density estimate in the offshore area is about one-half that value.

The school size estimate is about 200 animals, based on visual estimates of the size of schools seen during the aerial survey. The accuracy of these visual estimates has been confirmed by counts of individual dolphins from aerial photographs, and the accuracy of the counts from these photographs has been confirmed by counts of dolphins released from a purse seine (Allen et al. 1980). This estimated school size also includes an adjustment for the tendency of larger schools to be more readily visible at greater distances from the aircraft, and hence to be overrepresented in the sample.

Allen et al. (1980) also demonstrated that accurate school size estimates could be made from

ships. Although not used by Holt and Powers (1982), the mean school size estimated from research vessel sighting data was about 180, not significantly different from the value derived from aerial data described above. In contrast, the mean school size estimated from tuna vessel sighting data collected by scientific technicians was about 580, significantly higher ($P<0.001$) than the other two values. This difference implies either nonrandomness of the sample of dolphin schools encountered by the tuna vessels, or biases in the estimation techniques used by the technicians.

P_i for each of the 22 populations involved in the yellowfin tuna purse seine fishery can be estimated from data collected aboard either tuna vessels or research vessels. Fishing vessels encounter significantly more schools composed primarily of spotted and spinner dolphins than do research vessels. The reason for this difference is not known, but it is possible that fishing vessels encounter spotted and spinner dolpin schools more frequently than would be expected under random search because they are searching for tuna, which occur with these two schools more frequently than with other species of dolphins. Studies of the searching process of tuna fishing vessels are being conducted which should help resolve this question. Because the proportions P_i are different for unknown reasons, Holt and Powers (1982) gave several sets of estimates of total abundance, depending on the estimates of P_i from different combinations of the research vessel and tuna vessel data. Two sets of estimates are considered here (Table 1), one using research vessel data alone and the other using combined tuna vessel and research vessel data.

Aerial survey procedures used in the present population-size estimates are still being refined. For instance, a field study was completed in mid-

TABLE 1.—Population size estimates (thousands) at the beginning of 1979 for three populations of dolphins in the eastern tropical Pacific, using estimates of the species mix from research vessel data alone, and from combined tuna vessel data and research vessel data, with standard deviations in parentheses (Holt and Powers 1982).

Population	Research vessel data only	Fishing and research vessel data
Offshore spotted	1,682.0 (471.8)	2,775.0 (761.4)
Eastern spinner	292.7 (71.0)	292.9 (64.4)
Whitebelly spinner	216.0 (67.4)	380.4 (134.9)

[4]Hammond, P. S. (editor). 1981. Report of the Workshop on Tuna-Dolphin Interactions, Managua, Nicaragua, April 1981, p. 5. IATTC Spec. Rep. 4, Inter-Am. Trop. Tuna Comm., c/o Scripps Inst. Oceanogr., La Jolla, CA 92093.

1980 to determine the effect of sea state and sun position on the visibility of dolphin schools directly on the trackline. Data from this experiment, which have not yet been completely analyzed, will be of use in the design of future surveys and in the evaluation of earlier surveys.

INCIDENTAL KILL ESTIMATES

Incidental kill (K_t) of dolphins in year t is estimated by multiplying the mean kill of dolphins per set in year t (KPS_t) by the total number of net sets involving dolphins made by the tuna fleet in year t ($NSETS_t$), as

$$K_t = KPS_t \ NSETS_t. \qquad (6)$$

These estimates are obtained for each year with the data stratified by vessel fish-carrying capacity, amount of tuna caught in the net set, and geographic location of the set, following the general approach described by Lo et al. (1982).

Kill rate information is available from a limited set of tuna fishing trips in the 1960's and from a more extensive set in the 1970's collected by scientific observers placed aboard a large proportion of the U.S. fishing vessels. To illustrate the data, some mean kill rates, stratified by amount of tuna caught, are shown in Table 2. Higher kill rates are apparent in successful (>¼ ton tuna caught) than in unsuccessful (<¼ ton tuna caught) sets, as are marked declines in kill rates over time. Numbers of dolphin sets and fishing trips on which observations of numbers of dolphins killed were made are shown in Table 3.

Observations of the numbers of dolphins killed in the 1960's were made by both the crew and the scientists. Although few observations were made, there is no consistent difference between kill rates reported by both types of observers (59 and 52, respectively); this suggests the presence of a noncrew-member observer had no significant effect on the kill rate of dolphins in the 1960's.

All data on kill rates of dolphins for the period 1971-78 were collected by noncrew-member scientists, precluding a direct comparison of kill rates between fishing trips with (observed) and without (unobserved) scientific observers for this period. Croom,[5] however, reported dolphin kill rates on a fishing trip in 1979 with no scientific observer on board; his kill rates were about 4 times higher than the average rate in 1979 for scientist-observed trips and were approximately 20 times higher than on previous and succeeding observed fishing trips by the same vessel and captain. This difference in mean kill rates was due to the significantly lower proportion of sets with few dolphins killed on Croom's trip than on the scientist-observed trips. For instance, the proportion of sets with zero dolphins killed was 0.23 on Croom's trip with 0.76 for observed trips.

Although limited information is available, it appears that kill rates on some unobserved vessels were higher in the late 1970's, and that this could result in the observed kill rates being lower than the actual rates. If there has been an "observer effect," it most likely occurred in the late 1970's, because regulations were adopted in the United States in 1976 requiring the use of certain dolphin-release procedures, and because scientific observers were then used to collect regulation compliance information. If kill estimates for the last few years were revised with this in mind, it would only slightly affect the calculations presented here, since the large number of animals killed through 1975 tends to dominate in Equation (2). However, such revisions to the kill estimates could markedly change our perception of the current rate of change of these populations.

In addition to the known direct kill of dolphins in the fishery, research has been conducted to estimate both the number of dolphins injured and released alive from the purse seines, and the possible number of dolphins which, while not exhibiting injuries, die or suffer reduced viability from stress of capture and handling in the purse seining operation. Observations of the number of injured dolphins have been made aboard tuna vessels since 1975; estimates of the number in-

TABLE 2.—Observed mean kill of dolphins per net set (KPS) by U.S. tuna purse seiners 1964-78, for successful and unsuccessful net sets, with sample sizes (N), from NMFS records.

Year	Successful sets (> ¼ t tuna)		Unsuccessful sets (< ¼ t tuna)	
	KPS	N	KPS	N
1964-72	55.7	343	7.9	25
1973	22.6	576	0.6	130
1974	15.7	753	2.4	261
1975	18.9	778	2.5	169
1976	16.1	627	5.7	126
1977	3.4	2,706	0.9	495
1978	4.2	1,434	3.9	249

[5]Croom, M. M. 1980. The tuna-porpoise problem: Management aspects of a fishery. M.S. Internship Rep., Marine Resour. Manage. Program, Oreg. State Univ., Corvallis, 41 p.

jured fluctuate around 4.8% of the number killed directly, ranging from 3 to 7%. The problem of stress-induced mortality or debility was explored in a workshop of experts on large mammal physiology and pathology, and research plans to approach this problem were developed.[6] Subsequently one aspect of this problem was examined with dolphin specimens collected aboard tuna vessels.[7] Reproductive tracts were examined for evidence of spontaneous abortion, and muscle tissue for myopathy; no evidence of either was found. No estimates of the magnitude of such effects have been made, and currently no research is underway to investigate stress-induced mortality. As a conservative measure, given our limited knowledge, I assume in the estimates of total dolphin mortality given here that all of the injured dolphins subsequently die of their injuries. Thus estimates of total kill of dolphins are the sum of the estimated numbers killed directly and the numbers injured.

Numbers of net sets made by the tuna purse seine fleet have been recorded by the Inter-American Tropical Tuna Commission (IATTC) from logbooks kept by the fishermen (Table 3). In the logbooks the type of each net set may be recorded, along with tuna catch, location, and other information. The three major types of sets are 1) those known to involve dolphins, 2) those known not to involve dolphins, and 3) those for which the data indicate neither the presence nor absence of dolphins. Types of sets not involving dolphins include "floating object sets" (e.g., a rope, board, log, etc.), a "school fish set" (i.e., a net set on tuna sighted at or near the surface), and a "porpoise set." The logbook data are incomplete, however, because some members of the fleet do not report and because, in some cases, only limited information was recorded by the fishermen. The logbook coverage rate, however, is high.

The data in columns D, N, and U in Table 3 have only recently become available, and analyses are proceeding to use this information directly to estimate the total number of sets made on dolphins. Preliminary results for the total numbers of sets for each year[8] are similar to

TABLE 3.—Number of tuna purse seine sets, 1959-78, (D) known to have been made on dolphins in the eastern tropical Pacific, (N) known not to have been made on dolphins, and (U) unknown if made on dolphins (IATTC text footnote 8), with (E) estimates of the total number of sets made on dolphins (Smith text footnote 3). Also shown are the numbers of observed fishing trips and purse seine sets on porpoise from NMFS records.

	Sets made				Sets	Trips
Year	D	N	U	E	observed	observed
1959	132	759	2,985	1,037	0	0
1960	1,644	1,256	7,390	5,696	0	0
1961	3,617	3,825	8,694	8,247	0	0
1962	2,886	8,830	4,337	4,060	0	0
1963	3,290	9,266	6,322	4,687	0	0
1964	5,933	7,681	4,745	8,090	67	2
1965	6,172	7,176	5,631	7,981	0	0
1966	5,443	7,001	5,247	7,250	28	1
1967	3,510	10,018	3,594	4,478	0	0
1968	3,833	8,988	1,642	4,271	15	1
1969	7,664	6,552	2,055	8,678	0	0
1970	7,912	9,692	1,664	8,552	0	0
1971	4,816	10,728	3,404	5,039	78	5
1972	8,193	4,682	3,514	9,036	272	12
1973	8,686	9,463	3,672	9,998	752	22
1974	7,955	11,669	4,835	8,539	1,120	36
1975	8,172	13,396	4,902	8,951	1,049	31
1976	7,481	17,789	5,184	7,910	1,295	45
1977	7,485	15,005	7,643	9,757	3,335	94
1978	5,174	21,527	5,639	5,910	1,771	102

those given in column E of Table 3, but the results are not yet available in the stratified form needed to estimate numbers killed, described below. Earlier estimates of the total number of sets made on dolphins (column U of Table 3) were obtained indirectly for the years prior to 1970, based on the catches of tuna, and include an adjustment for nonreported sets.

For the Period 1959-72

Estimating the annual rate of dolphin kill during the period 1959-72 is difficult because observations were few, especially in the early part of the period; consequently, extrapolation of information on kill rates is necessary. One effect on rate of kill is the development and improvement of the "backdown" dolphin-release procedure (Coe and Sousa 1972; Barham et al. 1977), by which the vessel moves in reverse during a short portion of the purse seine retrieval, thereby pulling the net out from under the dolphins. Barham et al. (1977) reported that the "backdown" dolphin-release procedure was developed aboard one vessel in 1959 and 1960, and transferred to a second vessel in 1961. Subsequently, the use of the procedure expanded rapidly within the fleet, although

[6]Stuntz, W. E., and T. B. Shay. 1979. Report on capture stress workshop, La Jolla, California, May 1979. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep. LJ-79-28, 24 p.
[7]Cowan, D., and W. Walker. 1979. Disease factors in Stenella attenuata and Stenella longirostris taken in the eastern tropical Pacific yellowfin tuna purse seine fishery. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep. LJ-79-32, 21 p.
[8]Inter-American Tropical Tuna Commission. 1981. Tuna-

dolphin investigations. Background paper 6, prepared for the 39th meeting of the IATTC, Paris, October 1981. Inter-Am. Trop. Tuna Comm., c/o Scripps Inst. Oceanogr., La Jolla, CA 92093, 17 p.

full use was not evident even by 1964. Comparing kill rates with and without "backdown" is complicated however, because the effectiveness of the release procedure has increased over time.

No information is available on kill rates from non-U.S. vessels during 1959-72, but the non-U.S. fleet was small. There is little reason to suspect that these kill rates were different, because fishermen of both fleets were still learning how to use purse seine gear for catching tuna in association with dolphins and how to release the caught dolphins.

The available kill rate data for this period were stratified, for use in Equation (6), by amount of tuna caught, size of the vessel, and frequency of use of the "backdown" procedure. The data were pooled across the years 1964-72 and extrapolated back to the years 1959-63 when no kill rate data were collected. These stratified kill rates were multiplied by the number of sets made on dolphins in each stratum to estimate the total number of dolphins, of all populations, killed directly in this fishery.

Estimating proportions of the total kill of dolphins from each population for this period is difficult because the yellowfin tuna purse seining was expanding westward and because data on the species of dolphins observed killed are available only for 1971 and 1972. Prior to 1969 this fishery operated shoreward of the range of the whitebelly spinner dolphin, primarily within the range of the eastern spinner and offshore spotted dolphins. The total kill estimates are prorated to population for the years 1959-72, based on observed proportions in the 1971-72 data of 70, 23, and 3% for offshore spotted, eastern spinner, and whitebelly spinner dolphins, respectively. The other 4% consisted of several species, primarily common dolphins, *Delphinus delphis*, which are not considered in this study. Although the tuna purse seine fishery was expanding seaward throughout the 1960's toward the range of the whitebelly spinner dolphin, a major seaward shift occurred in 1969. Lacking detailed data, I assume this year to be the first significant involvement of the whitebelly population.

Some additional data on the species of dolphins involved in each set has recently become available from the IATTC, suggesting a declining proportion of sets involving spinner dolphins and an increasing proportion involving spotted dolphins throughout the 1960's. Preliminary examination of these data indicates that the overall proportions of sets involving each species are not

greatly different from the 1971-72 observer data. Direct use of these new data will involve making a number of assumptions about species-specific kill rates.

Using the above proportions based on the 1971-72 data and increasing the estimates of total number killed by 4.8% to account for those dolphins possibly dying of injuries, I estimated the total numbers of dolphins killed, by population (Table 4). These are revisions of estimates used by the 1979 workshop (footnote 3).

TABLE 4.—Estimates of numbers (in thousands) of dolphins killed by all fleets in the eastern tropical Pacific, 1959-78, for three populations of dolphins (Smith text footnote 3).

Year	Offshore spotted	Eastern spinner	Whitebelly spinner
1959	71	27	0
1960	357	133	0
1961	402	150	0
1962	167	62	0
1963	183	69	0
1964	306	115	0
1965	337	126	0
1966	306	115	0
1967	206	77	0
1968	178	67	0
1969	365	122	15
1970	355	118	14
1971	176	59	7
1972	288	96	12
1973	131	32	33
1974	95	26	47
1975	105	45	34
1976	47	9	20
1977	22	5	5
1978	19	2	4

For the Period 1973-80

Substantially more data exist on kill rates for the period 1973-78 than for the period 1959-72. The 1973-78 data are more reliable because they were collected by NMFS employees trained specifically for obtaining kill information. Starting in 1974 fishing trips were randomly selected for observation to obtain a representative sample. Greater cooperation by the fishing fleet resulted in an increasing proportion of selected trips actually observed from 1974 to 1976. However, it was not until 1976 that fishing trips begun after July were sampled. In the early 1970's fishing tended to occur farther offshore later in the year; because kill rates are generally higher in the offshore areas, the failure to collect data from late-season trips probably resulted in an underestimate of actual dolphin kill rates in those years. This problem is partially accounted for by stratifying the data by area. The species composi-

tion of the kill was also recorded, allowing direct estimates of total kill of dolphins, from Equation (6), for each population.

The number of dolphins killed per set from 1973 to 1976 for successful and unsuccessful sets was about 18 and 3, respectively, a decrease from the 1964-72 levels of 56 and 8. The number killed in successful and unsuccessful sets in 1977 and 1978 was again lower, about 4 and 2, respectively (Table 2). These decreases occurred as U.S. regulations were developed and eventually implemented, and as methods for more effective use of backdown and other dolphin-release procedures were developed and used. The decreases in kill rates were apparently due, at least in part, to wider adoption of procedures for dolphin release.

The non-U.S. tuna purse seine fleet increased markedly during this period. First observations of the kill rate for this fleet were in 1979, which showed that the rate was very similar to that of the U.S. fleet (Allen and Goldsmith 1981). Given this similarity in 1979, it is reasonable to assume that during the earlier part of the 1970's the non-U.S. kill rate declined, as did the U.S. kill rate (Table 2), as dolphin-release technology developed by the U.S. fleet became known. If such a decline in the non-U.S. kill rate occurred, however, it would probably have been somewhat slower than that for the U.S. fleet, because of lack of legal pressure to reduce the incidental kill and time lags in technology transfer. Following the procedure developed by the 1979 workshop (footnote 3), I estimated the non-U.S. kill by assuming 1) the same kill rate in 1971-72 for the non-U.S. fleet as that observed aboard U.S. vessels in those years; 2) the same kill rate in 1973 for the non-U.S. fleet as that of the U.S. fleet in 1975; and 3) a linear convergence of the two rates toward the 1979 U.S. rate. Estimates of numbers of dolphins killed by non-U.S. vessels obtained under these assumptions are used here. However, additional study is needed, especially since the recorded kill rate for the non-U.S. fleet in 1980 was somewhat higher than that for the U.S. fleet (Allen and Goldsmith 1982).

These kill rates, stratified by vessel size, amount of tuna caught, and area fished, are used in Equation (6), along with the estimated number of sets on dolphins, to estimate total direct kill by population for each year. These estimates are then increased by 4.8% to account for dolphins assumed to die of their injuries (Table 4). The results in Table 4 are slight revisions of the estimates used by the 1979 workshop (footnote 3).

NET RECRUITMENT RATE ESTIMATES

Maximum net recruitment rate (R_m) is required to estimate historical abundance. This is calculated as the difference between gross production of calves and the natural mortality rate, assuming that natural mortality does not change, when a population is reduced substantially below its equilibrium level.

Gross Reproductive Rates

Gross recruitment rates can be estimated as the product of the female fraction of the population, the mature female fraction, and the annual pregnancy rates. Estimates of these parameters are given in Table 5, based on samples of dolphins collected by scientific observers aboard tuna vessels from 1973 to 1978. Two methods were used to estimate the annual pregnancy rate: The first method (I) is the observed proportion of pregnant females in the population divided by the gestation period; the second method (II) is similar, but uses additional information on frequency of nursing calves in the samples from each net set (Perrin et al. 1977a, b, c).

There are known sampling biases in these data for spotted dolphin because of the fishing process, partly accounted for by using data for spotted dolphin recruitment rates from only those sets where more than 40 dolphins were killed. In addition, the observed fraction of the mature, pregnant female dolphins has varied among years, with a general decline in offshore spotted dolphin and a large degree of variability in eastern spinner dolphin.

Age-specific effects are not accounted for in the analyses so far, however, particularly the

TABLE 5.—Proportion of sampled dolphins (female and mature) of three populations and estimates of annual pregnancy rate (P) and gross reproductive rate (G), using two methods.[1] See text for details.

| | | | Annual production | | | |
| | Proportion | | Method I | | Method II | |
Population	Female	Mature	P	G	P	G
Offshore spotted	0.56	0.56	0.38	0.119	0.32	0.100
Eastern spinner	0.51	0.43	0.34	0.075	0.45	0.099
Whitebelly spinner	0.51	0.52	0.36	0.096	0.33	0.088

[1]Henderson, J. R., W. F. Perrin, and R. B. Miller. 1980. Rates of gross annual production in dolphin populations (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific, 1973-1978. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep. LJ-80-02, 51 p.

lower pregnancy rate that probably occurs in older animals. New methods are being developed for age determination, and an effort is being made to apply these methods to age the samples of dolphins. With accurate data on age of animals, a more detailed examination of sampling biases will be undertaken.

Natural Mortality Rates

No direct estimates of natural mortality rates exist for the eastern Pacific dolphin populations, as might be obtained from tagging data or from a sampled age structure. Ohsumi (1979) presented a statistical relationship between natural mortality rate and body length for cetaceans, from which can be derived an annual, natural mortality rate of around 0.14 for the eastern Pacific dolphin populations. However, this estimate is obtained by extrapolating the relationship outside the range of his data, and consequently is unreliable.

Another method of estimating natural mortality rate is from information on gross reproductive rate for a population in equilibrium with its environment, assuming natural mortality does not change with population size. This approach was used in the 1976 workshop (footnote 2). An estimate of gross reproductive rate of 0.09 (Kasuya et al. 1974) for a population off Japan, thought to be lightly exploited, was used as the natural mortality rate estimate for the eastern tropical Pacific populations. It now appears that the population off Japan had, in fact, been exploited to a greater degree than was thought, and that there is segregation of prepubertal dolphins into separate schools (footnote 3, p. 41). The assumption, consequently, of a natural mortality rate of 0.09 is probably not valid.

In the 1979 workshop (footnote 3), estimates of the gross reproductive rate of lightly exploited Southern Hemisphere populations of spotted and spinner dolphins in the eastern tropical Pacific were used as estimates of natural mortality rates. These rates were 0.098 and 0.067 for spotted and spinner dolphins, respectively.

Net Rates

Net recruitment rates for the offshore spotted, eastern spinner, and whitebelly spinner dolphin populations can be estimated as the differences between the gross reproductive rate estimates, listed in Table 5, and the corresponding natural mortality rate estimates given above. Using method I estimates of pregnancy rates, one obtains estimated net reproductive rates of 0.021, 0.008, and 0.029 for these three populations, respectively. Using method II estimates of pregnancy rates, one obtains estimates of 0.002, 0.032, and 0.021, respectively. These highly variable estimates are unsatisfactory, because they are based on data with known sample biases, and they differ among populations in unexpected ways. In particular, it is not expected that the net reproductive rate of the whitebelly spinner dolphin, which has been relatively less exploited, should be higher than that of the more heavily exploited eastern spinner dolphin population.

Due to these uncertainties, specific point estimates were not obtained by the 1979 workshop participants. Rather, a range of values from 0.0 to 0.04 were considered equally likely, given the available information. The lower value of 0.0 was selected by the 1979 workshop to reflect uncertainties about unexpected changes in some reproductive rates, and the small magnitude of the estimates of net reproductive rates. This range compares with the estimates from the 1976 workshop of 0.02-0.06, with a midpoint estimate of 0.04. Although higher rates of increase of cetacean populations have been reported, contrary to the conclusions in the 1979 workshop report, there are no reliable estimates of rates of increase for dolphin populations which can be used with confidence. Pending better information, the range of estimates considered in the two workshops will be used here, recognizing that higher rates may be possible.

Rate Dependent on Population Size

The evidence on which to base an estimate of the value of Z in Equation (3) for dolphin populations is limited. Fowler (1981) argued that for large, long-lived mammals, Z is greater than unity. He based this conclusion on a review of empirical data, primarily from terrestrial populations, and on an analysis of the demographic constraints which come with long life and extended parental care. McCullough (footnote 3, p. 8) gave preliminary estimates of maximum net productivity level ($MNPL$), and hence Z, for four large terrestrial mammal populations. His estimates agree with Fowler's conclusions that Z is greater than unity, and that later reproducing animals would have higher values of Z.

The 1976 workshop (footnote 2) concluded that the available information implies *MNPL* is within the range of 50-70% of the equilibrium population size, corresponding to values of Z from 1 to 5.1. The 1979 workshop recognized that "There had been a shift of scientific opinion in recent years [since 1976] towards accepting the idea that relative net productivity in mammals, especially large, K-selected species, is a non-linear function of population size," (footnote 3, p. 7) and concluded that *MNPL* for these dolphin populations is probably in the range of 65-80% of the equilibrium population size (Z from 3.5 to 11.5). I consider the values for *MNPL* of 50-80% (Z from 1 to 11.5) of equilibrium population size in order to explore the sensitivity of the calculations to this uncertainty.

HISTORICAL TRENDS IN ABUNDANCE

Estimates of population sizes prior to 1979 from Equations (2) and (3) for each population are shown in Table 6. Values are given using 1) two different estimates of present (1979) abundance (from combined research vessel and fishing vessel data, and from research vessel data alone), and 2) the parameters *MNPL* = 65% and $R_m = 0.03$. For this range of parameter values, the offshore spotted dolphin population in 1959

was between about 4,800,000 and 5,600,000 animals. The eastern spinner dolphin population in 1959 numbered about 1,500,000, while the white-
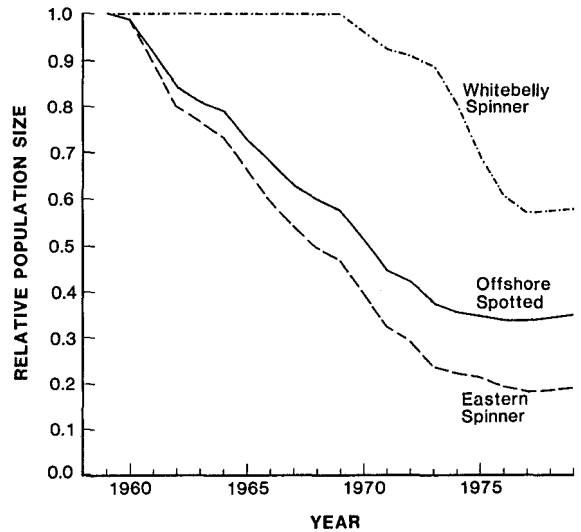

FIGURE 1.—Relative population sizes of whitebelly spinner, offshore spotted, and eastern spinner dolphins, 1959-79, using population estimates based on species proportions from combined research and fishing vessel data, and assuming $R_m = 0.03$ and *MNPL* = 65% of equilibrium abundance. Population sizes are relative to estimated population sizes in 1959.
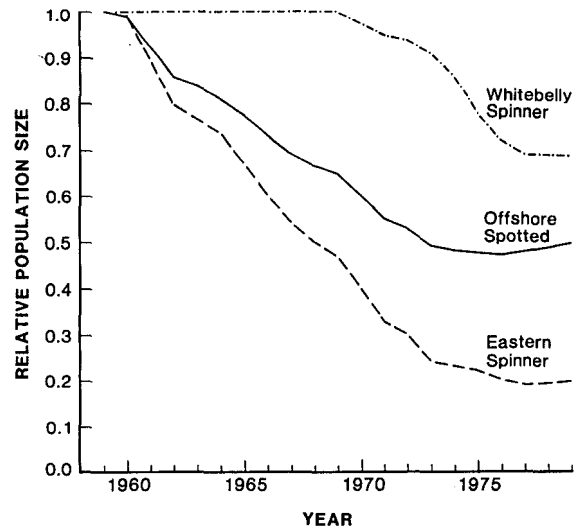

FIGURE 2.—Relative population sizes of whitebelly spinner, offshore spotted, and eastern spinner dolphins, 1959-79, using population estimates based on species proportions from research vessel data alone, and assuming $R_m = 0.03$ and *MNPL* = 65% of equilibrium abundance. Population sizes are relative to estimated sizes in 1959.

TABLE 6.—Estimates of population size (in thousands) of offshore spotted, eastern spinner, and whitebelly spinner dolphins from 1979 back to 1959, using Equations (2) and (3) and parameters *MNPL* = 65% and $R_m = 0.03$. 1979 estimates are based on species proportions from (FR) combined research vessel and fishing vessel data and (R) research vessel data alone.

Year	Offshore spotted		Eastern spinner	Whitebelly spinner	
	FR	R	FR = R	FR	R
1979	2,775	1,682	293	380	216
1978	2,719	1,653	287	376	215
1977	2,668	1,628	283	373	214
1976	2,673	1,629	284	386	229
1975	2,675	1,686	320	434	258
1974	2,679	1,732	336	456	301
1973	2,754	1,824	358	486	331
1972	2,967	2,046	443	494	340
1971	3,064	2,164	488	499	345
1970	3,340	2,457	591	512	358
1969	3,264	2,756	695	527	373
1968	3,720	2,865	742	527	373
1967	3,844	3,001	799	527	373
1966	4,071	3,239	893	527	373
1965	4,335	3,520	998	527	373
1964	4,574	3,754	1,092	527	373
1963	4,695	3,879	1,141	527	373
1962	4,803	3,991	1,185	527	373
1961	5,169	4,358	1,323	527	373
1960	5,519	4,708	1,454	527	373
1959	5,590	4,779	1,481	527	373

belly spinner dolphin population in 1969 numbered between 400,000 and 500,000. The offshore spotted and eastern spinner dolphin populations declined rapidly in the 1960's and early 1970's in the face of kills which were, for example, on the order of 7-12% of the 1965 population sizes. The whitebelly spinner dolphin population declined most rapidly in 1974 when the kill was between 11 and 16% of its population size.

These estimates of absolute population sizes are shown in Figures 1 and 2 relative to the equilibrium population size (N_t/N_p), so that the trend in abundance of these populations can be examined. For all of the parameter values considered, these dolphin populations have declined substantially relative to their pre-exploitation sizes.

The ratio of 1979 to pre-exploitation population sizes for different values of R_m and $MNPL$ (and hence Z) shows the sensitivity of the calculations to changes in parameter estimates (Table 7; Figs. 3, 4). The value of $MNPL$ when R_m is zero

is not meaningful, as the estimate of pre-exploitation population size (Equation (2)) collapses to the sum of the present population size estimate and the total numbers killed over all years. This is reflected in Figures 3 and 4 in the convergence of the lines when R_m is zero.

TABLE 7.—Estimates of 1979 relative population sizes of offshore spotted, eastern spinner, and whitebelly spinner dolphin populations, using two estimates which differ in species proportions from (FR) combined fishing and research vessel data and from (R) research vessel data alone, for ranges of maximum net recruitment rate (R_m) and maximum net productivity level ($MNPL$).

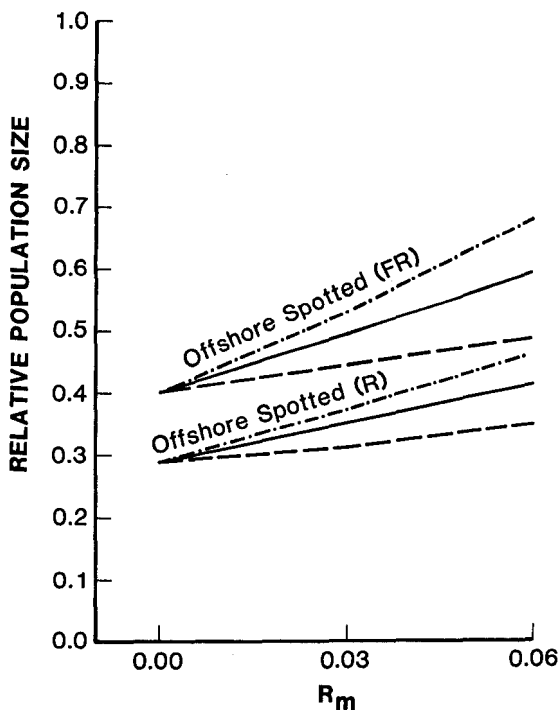| R_m	$MNPL$ (%)	Offshore spotted		Eastern spinner	Whitebelly spinner	
		FR	R	$FR = R$	FR	R
0.00	—	0.40	0.29	0.17	0.66	0.53
0.03	50	0.45	0.32	0.18	0.69	0.55
	65	0.50	0.35	0.20	0.72	0.58
	80	0.53	0.37	0.21	0.77	0.61
0.06	50	0.49	0.35	0.20	0.71	0.57
	65	0.60	0.42	0.23	0.78	0.63
	80	0.68	0.47	0.25	0.86	0.69

FIGURE 3.—Population size of offshore spotted dolphins in 1979 relative to 1959 (N_{79}/N_{59}) as a function of maximum recruitment rate ($R_m = 0, 3, 6\%$) using two current population estimates which differ in species proportions from (FR) combined fishing and research vessel data and from (R) research vessel data alone. $MNPL$ values of 50% (dashed lines), 65% (solid lines), and 80% (dot-dashed lines) are shown.
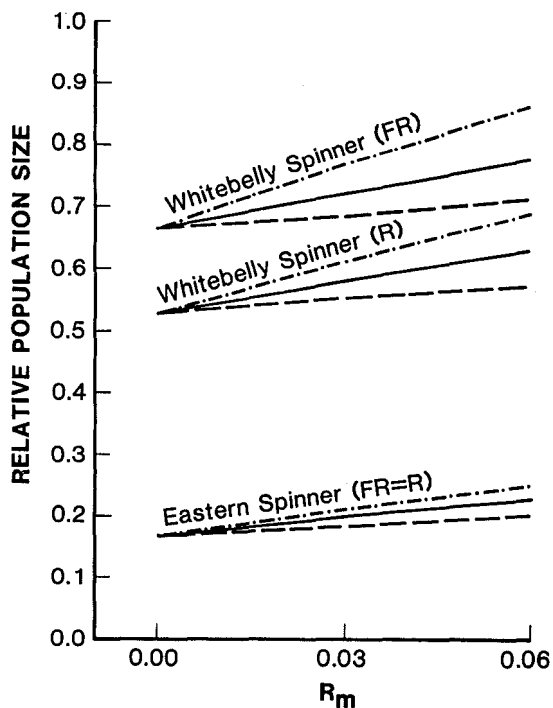

FIGURE 4.—Population sizes of eastern spinner and whitebelly spinner dolphins in 1979 relative to 1959 (N_{79}/N_{59}) as a function of maximum recruitment rate ($R_m = 0, 3, 6\%$) using two current population estimates which differ in species proportions from (FR) combined fishing and research vessel data and from (R) research vessel data alone. $MNPL$ values of 50% (dashed lines), 65% (solid lines), and 80% (dot-dashed lines) are shown.

DISCUSSION AND CONCLUSIONS

The three populations of dolphins involved with the yellowfin tuna purse seine fleet in the eastern tropical Pacific have declined since 1959 and the decline was not arrested until recently (Figs. 1, 2). Assuming the historical kill level, and the central values for R_m and $MNPL$, the whitebelly spinner dolphin population has declined to between 58 and 72% of its pre-exploitation levels; the offshore spotted dolphin population has declined to between 35 and 50% of its pre-exploitation size; and the eastern spinner dolphin population has declined to around 20% of its pre-exploitation size.

Examination of Figures 3 and 4 shows that the numerical values of the estimates of relative abundance in 1979 for offshore spotted dolphin and whitebelly spinner dolphin are relatively more sensitive to changes in the maximum net recruitment rate and the maximum net productivity level parameters than are the estimates for the eastern spinner dolphin. Also, the sensitivity of these calculations to the maximum net productivity level increases markedly as the value of the maximum net recruitment level increases. The sensitivity (in percent change) in the ratio of present to pre-exploitation abundance, however, is largest for the offshore spotted dolphin and least for the whitebelly spinner dolphin. This is due in part to the shorter time span over which the whitebelly spinner dolphin has been exploited, and in part to the lower $\frac{N_t}{N_p}$ ratio for the eastern spinner dolphin ratio, which makes smaller differences result in a larger percentage.

Although there are a number of uncertainties about specific parameter estimates used in these calculations, the general declines in abundance change relatively little over the ranges of parameter estimates explored. For example, rather rapid declines in the 1960's, followed by decreasing rates of decline in the 1970's, are evident for all parameter values considered. Specific aspects of these declines in abundance, however, depend to a greater degree on the actual parameter values. For example, the estimated changes in population sizes from 1975 to 1978 vary with the specific values of maximum net recruitment rate, while the estimated changes in population sizes in the 1960's are relatively insensitive to this parameter.

In order to improve our estimates of reproductive and mortality rates, a complete review of vital rates for these dolphin populations and for cetaceans in general should be carried out. Several approaches to this problem have been identified, including a detailed review of the eastern tropical Pacific dolphin data and of the existing data for other cetacean populations. Given the gaps in our knowledge of cetacean reproductive processes, analyses of alternate mathematical models of such processes will be fruitful.

Although improvements in estimates of abundance and kill levels are needed, these areas are generally much better understood than the recruitment process. Population-size estimation techniques are still being improved upon; current emphasis is on testing the assumptions needed in applying line transect theory to aerial sighting survey data and in estimating dolphin school size. Future work will emphasize improved shipboard sighting methodology for possible application of line transect theory.

Marked improvements in the estimates of numbers of dolphins killed are not anticipated; key areas needing additional information are the kill rates both in the non-U.S. fleet and on unobserved fishing trips. Neither of these areas is readily amenable to study, although further analysis of the kill rates on unobserved trips may provide some basis for exploring this uncertainty. The possible levels of indirect mortality or debility due to the stress of chase and capture are also of concern. Because of the large numbers of dolphins captured and released each year, even very low rates of indirect mortality could have a significant effect on the population.

ACKNOWLEDGMENTS

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