UNITED STATES DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
NATIONAL MARINE FISHERIES SERVICE

Southeast Fisheries Center
75 Virginia Beach Drive
Miami, Florida 33149

April 3, 1980

TO: F/SER - Dr. Don Eckberg

THROUGH: F/SECx4 - Dr. Herb Kumpf

FROM: F/SECx4 - Frederick H. Berry

SUBJECT: Turtle Population Model and Estimates

Attached is the SEFC response to your verbal request for an evaluation of your Cape Canaveral loggerhead turtle population estimate. Also included is a descriptive model of turtle populations as applied to our SE geographical region. These are drafts.

The following individuals and their staff have worked long and hard and deserve credit for providing this input:

Dr. Joe Powers, Chief
Fisheries Data Analysis Division, Miami

Charles McVea, Manager
Sea Turtle Habitat Survey Project, Pascagoula

Ray Conser, Chief
Analytical and Technical Support Branch, Miami

Nancy Thompson, Leader
Turtle Data Base and Population Modeling Project, Miami

Attachments: 4

cc: W. Fox
A. Kemmerer
W. Richards
F. Berry

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TO: F/SECx4 - Herb E. Kumpf

FROM: F/SEC1 - Joseph E. Powers *Joseph E. Powers*

SUBJECT: Turtle Population Analysis

With this memorandum, I am addressing the problems of turtle population analysis being faced by the Marine Mammals and Endangered Species Program (MMESP) of the SEFC. This memo has been precipitated by the involvement of the Fisheries Data Analysis Division (FDAD) of the Miami Laboratory in Several activities. In particular, these activities have included: planning for aerial nesting surveys in the Atlantic and Gulf states, assessing possible impacts of dredging activities on turtles in the Cape Canaveral Ship Channel, utilizing data obtained from the ongoing trawl sampling in the Canaveral Channel, and discussions of long-term data needs for assessing impacts on turtle stocks. In this memo I will comment on the above activities and attempt to provide direction to SEFC efforts in turtle population analysis. To do this I will present a discussion of an initial assessment of the possible impact of dredging on Cape Canaveral turtles done by Don Ekberg (memo to file: Feb. 7, 1980, attached) and a reanalysis of this assessment done by the FDAD; I will comment on sampling methods and design in the Canaveral area; and finally discuss the data gaps in turtle population analysis in general, and likely methods for filling those gaps.

Cape Canaveral Assessment

In the attached analysis by Don Ekberg, the numbers of loggerhead turtles (Caretta caretta) which are subject to mortality from dredging activities in the Cape Canaveral Shipping Channel were estimated. The number of turtles was then compared to estimates of the number of loggerheads in each life stage which are produced by the breeding females of the Cape Canaveral area. Ekberg's initial conclusions may be summarized as:

1) between 400 and 2,000 loggerhead turtles occupy the shipping channel; essentially, all of these are sub-adults and all will experience mortality due to dredging;

2) the "stock" of breeding loggerhead females in the Cape Canaveral area produces an estimated population of 7,900 sub-adults and 4,250 adults;

3) between 5 and 25 percent of the sub-adult population in the Canaveral area could be killed by the proposed dredging.

4) Ekberg developed these conclusions by using the trawl sampling data to estimate number of sub-adults in the channel (swept area method): then reported values (published and unpublished manuscripts and personal communications) of number of nesting females, hatchling survival, age of maturity, maximum age, age of sub-adults, eggs per nest, within season nesting frequency, and sex ratio. These parameters were combined into a survival curve model which was used to obtain the number of sub-adults in the Canaveral area. The survival model is based upon a report of Richardson (presented at First World Congress on Sea Turtles, Wash. D. C., Nov. 1979) for loggerheads in Georgia.

In reanalyzing this problem, we have broken the problem into: (1) estimating the number of turtles by age group in the Cape Canaveral Ship Channel, and (2) projecting the number of turtles by age group in the Canaveral Area.

Turtles in the Channel

The Mississippi Laboratories (SEFC) have conducted trawl surveys for turtles in the Canaveral Channel since October 1978. From these data they have developed estimates of loggerhead turtle density and numbers in the Channel. The method of estimation is based on a swept area technique in which density was calculated as the number of turtles caught relative to the bottom area actually fished by the trawl. Density was corrected for the efficiency of the trawl (which was determined from a separate trawl experiment). Densities were expanded to total number presented each sampling site by multiplying by the hectares per sampling site in the Channel. The results are in Table 1. It should be noted in Table 1 that the sampling effort was not equivalent between months. In particular, the May estimate of 21 turtles resulted from problems in implementing the particular trawler's sampling gear. The monthly density data 1978-1980 (not given herein) did not indicate any demonstrable seasonality in the abundance of turtles. Recognizing these caveats, the unweighted mean over all months was calculated, yielding a mean of 415 turtles and a standard error of the mean of 88.

Note that the above standard error is probably a lower bound for the estimate, since variation in catch efficiency has not been quantified. The above estimates were based upon a trawl efficiency estimate of approximately 46%from trawl experiments conducted by the Mississippi Laboratory (SEFC); i.e., 46% of the turtles in the path of the trawl will be caught. This efficiency is likely to be reduced by winds, currents, light and other environmental conditions to a great degree. Therefore, as further experimentation on trawl efficiency is done, the resulting estimate may change considerably. For example, the impact of light conditions on efficiency may be seen by comparing catch-per-trawl statistics between day and night trawls for the March 1980 samples. The mean number of turtles caught per night trawl was 7.57 (standard error of the mean was 1.24). Conversely, the mean for day trawls was 5.29 (standard error 1.31). These means are not significantly different in a statistical sense. However, the direction of the effect (night trawls captured at a higher mean rate) indicates the possible impacts of efficiency variation.

Therefore, we conclude that precise trawl efficiency statistics stratified for appropriate exogenous conditions are needed for truly unbiased estimates of density to be generated from trawl samples.

The age (size) composition of the trawl samples are shown in Table 2. The distribution is fairly constant from month to month; therefore, estimates of the total number of turtles by age group in the channel at any given time were obtained by multiplying the relative frequency by the mean number present over all months ($\bar{x}$=415), yielding:

Juveniles = .0035 x 415 = 1
Sub-adults = .7435 x 415 ≐ 309
Adults = .2531 x 415 = 105

The standard errors for these estimates; (noting problems with estimates of the variation in efficiency) are:

Standard error of Juveniles = 1
" " " Sub-adults = 66
" " " Adults = 24

Additionallly, one sub-adult Atlantic Ridley was captured in the March 1980 samples; thus, indicating that this species is sometimes present in the Channel. Since this species was caught at a rate half of that of juvenile loggerheads (i.e., all samples 1978-1980 produced two juvenile loggerheads and 1 Atlantic Ridley: see Table 2), we can estimate the abundance of Ridley's in the Channel to be one-half of that of juvenile loggerheads, i.e., the abundance is 0.5. In essence, 1 Ridley is expected to be in the Channel every other sampling period.

The above has been based upon the trawl data. Trawl sampling of turtles was also used as a means for placing tags on the turtles. The relative infrequency of recaptures which occurred in these trawls would indicate that many turtles are present in the Channel and, thus, trawl efficiency is low. An alternative, and equally likely, hypothesis is that the assumption of random mixing and no emmiagration of mark-recapture methods are not met. We can make no distinction between these hypotheses at this time.

Table 1. Estimates of turtle abundance in numbers in the Cape Canaveral Ship Channel by month using pooled 1978-1980 data from SEFC trawl samples

	Sampling Site [1]									
Month	1	2	3	4	5	6	7	8	# Turtles sampled	Total Abundance
Jan	0.0	0.0	0.0	0.0	0.0	8.54	47.69	214.0	55	270.0
Feb	0.0	0.0	0.0	0.0	0.0	34.31	83.46	166.2	120	284.0
March	0.0	0.0	0.0	0.0	0.0	0.0	27.64	362.4	196	390.0
April	0.0	0.0	0.0	0.0	0.0	0.0	0.0	135.0	5	135.0
May	0.0	0.0	0.0	0.0	0.0	0.0	21.0	0.0	1	21.0
June	0.0	52.0	0.0	0.0	0.0	57.0	173.1	298.7	52	580.8
July-August:	No samples									
Sept	0.0	0.0	0.0	0.0	0.0	0.0	130.1	288.0	37	418.0
Oct	0.0	0.0	0.0	0.0	0.0	51.0	290.0	361.0	21	702.0
Nov	0.0	0.0	0.0	0.0	0.0	51.0	174.0	145.0	20	370.0
Dec	0.0	0.0	0.0	0.0	0.0	0.0	251.0	725.3	62	976.3

[1] Sampling Site Descriptions:
1. Barge Canal
2. West Basin
3. Middle Basin
4. Inner Reach
5. East Basin
6. Middle Reach
7. Outer Reach
8. Extended Outer Reach

Table 2. Age (Size) frequency by month of loggerheads using pooled 1978-1980 data from trawl samples in the Cape Canaveral Ship Channel

Month	Age Group 1/						
	Juvenile		Sub-adult		Adult		Total
	Freq.	%	Freq.	%	Freq.	%	Freq.
Jan	0	0.00	49	89.09	6	10.91	55
Feb	0	0.00	104	86.67	16	13.33	120
March	2	1.02	139	70.92	55	28.06	196
April	0	0.00	0	0.00	5	100.00	5
May	0	0.00	1	100.00	0	0.00	1
June	0	0.00	27	51.92	25	48.08	52
July-August:	no data						
Sept	0	0.00	31	83.78	6	16.22	37
Oct	0	0.00	15	71.43	6	28.57	21
Nov	0	0.00	15	75.00	5	25.00	20
Dec	0	0.00	42	67.74	20	32.26	62
TOTAL	2	0.35	423	74.34	144	25.31	569

1/ Juvenile $\leq$ 50.8 cm, Sub-adult = 50.9 to 76.2 cm, Adult $\geq$ 76.3 cm

Turtles in the Canaveral Area

The technique for generating the number of loggerheads in each age-group in the Canaveral area, based upon the number of breeding females, relies on a survival projection model (Richardson (1979) and attached formulae). Ekberg parameterized this model to do his initial analysis. In our reanalysis, we examined the techniques of Ekberg, attempted to establish the source of his parameter estimates and refined those estimates, where possible. We then did a sensitivity analysis to test the impact of alternative parameter sets on the number of trutles generated by the model. The parameters used by Ekberg and ourselves are given in Table 3. The following is a discussion of each parameter.

No. Nesting Females: Ekberg gave a value of 850. In 1979 Ehrhart (personal communication) encountered 847 breeding female turtles in the Canaveral Area while conducting a tagging experiment of nesting females. This sample indicated that there were approximately 1200 nesting females in the area (Ehrhart, personal communication). We used Ehrhart's estimate, as well as arbitrary values of 1050 and 1350 to depict the possible variation in the estimate; this would be equivalent to a coefficient of variation at about 10%.

Sex Ratio: There appears to be no documented deviation from a 1:1 sex ratio for loggerheads. Owens, Hendrickson, Lance and Collard (1976, Am. Zool. 16:253) reported a female dominated sex ratio of 33:1 for green sea turtles as determined biochemically from random samples of sub-adults raised from eggs collected from seven geographical sources. However, the variation in sex ratio between areas was extremely large. Therefore,a single cohort (even a relatively large cohort) might exhibit a sex ratio different form 1:1 when the sex ratio of the population was unity. In our simultaneous sensitivity analysis we only considered a 1:1 ratio. The effect of alternative ratios acting alone will be discussed later.

Percent Adult Females Nesting per Year: estimates of the breeding cycle are often given as once every 2, 3 or 4 years (Richardson (1979) Ehrhart (1978). This would indicate from 25 to 50% of the females breed per year. We tested values of 30, 40 and 50%, which includes Ekberg's estimate of 40%

Number of Eggs/Nest: For loggerheads this was specified as 100. Richardson (1979) and Ehrhart (1978) reported between 100-120 per nest. These is a quantity with is fairly easy to measure,thus we considered that variation was small. Therefore, we only used one alternative: 100 eggs/nest.

Number of Nests/Year: Ekberg used 3.2 nest/year per breeding female. Richardson (1979) reports 2-3. We tested two alternatives: 2 and 3.2.

Survival Rate of Hatchlings: Richardson (1979) uses 0.10 as the proportion of eggs which produce hatchlings entering the sea. He also notes that this is highly variable. We utilized 0.05, 0.10 and 0.15 as alternatives (Ehrhart, personal communication).

Ages: Virtually nothing is known of true ages of loggerheads, because an aging method is not available. Richardson (1979) reports one female who has nested over a span of 15 years. He indicates that the breeding span may be as much as 25 years. The age at maturity and that at the beginning of the sub-adult phase are equally ill-defined. The alternatives given in Table 3 provide a wide range to reflect the "conventional wisdon."

Table 3. Parameter estimates used by Ekberg and in this present analysis

Parameter	Symbol	Ekberg Estimate	Alternatives in this Study
No. Nesting Females	NNF	850	1200; 1050; 1350
Sex Ratio	R	1:1	1:1
Percent Adult Females Nesting per year		40	30; 40; 50
Number of Eggs/Nest	NEN	100	100
Number of Nests/Year for each Adult Breeding Female	F	3.2	2.0; 3.2
Survival Proportion of Eggs to Hatchlings Entering the Sea	B	0.10	0.05; 0.10; 0.15
Ages (Years)			
Age at Beginning of Sub-Adult Stage	t_{SA}	4	3;4;5
Age at Adulthood	t_A	8	6;8;13
Age at which 10 turtles are left, i.e., maximum age	t_{MAX}	26	26; 33
Relationship between Sub-Adult Mortality (M_{SA}) and Adult Mortality (M_A) i.e., $M_{SA} = \gamma M_A$	γ	1.0	1.0; 1.2

Relationship between Adult and Sub-Adult Mortality: The survival projection model was originally founded with the assumption that sub-adult and adult mortality rates were equal (γ=1, see Table 3). We also tested the alternative that sub-adult mortality was 20% higher than adult (γ= 1.2). This was an orbitrary choice, the direction of which is consonant with many animal populations. However, it was used to illustrate qualitative changes in a bundance, only.

Of the parameters in Table 3 (for a closed stable population), we tested every combination in the model. Some of these resulted in infeasible results, i.e., negative mortality rates. These were eliminated from further consideration. Also, most animal populations exhibit mortality rates for young age-groups which are as least as great as those of older age groups. If we restrict ourselves to this criteria (which has not been corroborated for loggerhead turtles), we can refine the range of results of the model, as well. The results of our sensitivety analysis as compared to Ekberg's point estimate are given in Table 4. As can be seen, an extremely wide range of numbers per age group can be generated from combinations of reasonable parameter estimates.

A great deal of the variability of results from the choice for the ages of adulthood, sub-adulthood and maximum age. These ages specify the slope of the survival curve and, thus, the mortality rates and the number in each age-group. The impact can be seen in Table 5 comparing column (3) with column (2). Column (3) is the result of the model projection using the same parameters as colunm (2), except the maximum age is 33 instead of 26 years. By doing so, the number of sub-adults is reduced to one-half of column (2). Similar sensitivities are shown in columns (4) and (5); where the first sub-adult age is changed from 4 to 5 years and where the first adult age is changed from 8 to 6 years, respectively. To accommodate the possibility that the sex ratio could be female dominated by as much as 33:1, as reported by Owens, et. al. (1976) for green turtles, this ratio was tested with the base parameter set (Table 5; column (7) as compared to comumn (2). The net effect of a female dominated sex ratio is that the total members per age group are reduced. This could be a significant factor if the domination is as much as 33:1. However, we repeat that no evidence exists for this ratio in loggerheads.

The wide variation in predictions results in part, from the nature of the model. Many of the parameters of the model are extremely critical to the assessment, i.e., the model is not robust to these parameters. In particular, the ages at which life stages are reached are sensitive. However, as was mentioned before, no effective way of aging turtles exists. Even if a method did exist, the model would still be extremely sensitive to the normal variability of the aging method. It is the conclusion of this analysis that the survival projection method does not provide a usably precise estimate of numbers by age-group, and it is unlikely to do so in the future due to the demands of the model for very precise parameter estimates.

Therefore, we must look for alternatives. One alternative is to obtain unbiased estimates of the relative distribution of age-groups and then try to match this distribution with a relative distribution from the survival projection model. This would probably limit the number of combinations of feasible parameters somewhat; but this would still result in wide ranges for parameter estimates and, hence, in the number per age-group.

Table 4. Number of juvenile, sub-adult and adult loggerhead turtles in the Canaveral area obtained from the survival projection model. Parameters utilized are in Table 3.

	Ekberg Parameter Set Number of Turtles	Sensitivity Analysis of Alternative Parameters [1] Range of Number of Turtles
Juveniles	44,919	13,703 - 165,371
Sub-Adults	7958	715 - 68,313
Adults	4250	4200 - 9,000
TOTAL Adults & Sub-Adults	12,208	4915 - 64,443

[1] Includes only results where the juvenile mortality rate was greater than or equal to sub-adult and adult mortality rates.

Table 5. Examples of model projection results using various parameter sets, changing one parameter at a time. See Table 3 for alternative parameter sets and symbol definitions

	(1) Ekberg Parameter Set	(2) Base Parameter Set, i.e. Ekberg Set with NNF=1200	(3) Base Set with t_{MAX}=33	(4) Base Set with t_{SA}=5	(5) Base Set with t_A=6	(6) Base Set with γ=1.2	(7) Base Set with R=3381 Females
Juveniles							
Number	44,919	67,402	52,266	76,509	52,951	73,101	49,017
% Annual Mort.	41.37	38.69	49.73	36.15	49.46	35.08	52.45
Sub-Adults							
Number	7,958	12,924	6,872	8,204	3,937	14,835	5,049
% Annual Mort.	23.08	24.89	17.28	24.89	22.21	29.06	21.34
Adults							
Number	4,250	6,000	6,000	6,000	6,000	6,000	3,091
% Annual Mort.	23.08	24.89	17.28	24.89	22.21	24.89	21.34

Another alternative is to obtain direct estimates of absolute number of turtles by age-group of turtles in the Canaveral area. This could be done by a combination of direct survey methods. We feel that this would provide the best data for present methods of analysis.

There are two other problems with the survival projection model. First, it is assumed that the age distribution is stable, i.e., that the number of breeding females this year is indicative of the number of females that produced the present population of juveniles, sub-adults and adults. We have no data to evaluate this assumption. However, any animal population whose man-induced mortality is variable from year-to-year and whose mortality is not cross-sectional with respect to age would be unlikely to have a stable age distribution. Secondly, there is a tacit assumption that the female breeding in the Canaveral area are producing the turtles which may be impacted in the channel. In fact, there are many alternative hypotheses which could describe their life history. Two of these are:

1) Females breeding at Canaveral may breed at other sites during the two to four year cycle; thus, this turtle "stock" may include sub-adult and adult individuals at some other, unknown, locations; this has never been seen in loggerheads; however, never has the converse been shown , either; and

2) The channel may be a haven for migrating turtles arising from breeding stocks at a variety of locations,

The lack of recaptures of marked animals in the Ship Channel could indicate that the channel is a nesting place in a migration route. However, as mentioned before, this could be explained equally logically as a result of an overestimate of the travel effeciency.

In conclusion, no data are available to indicate where the turtles go after they hatch from the Cape Canaveral nesting areas. Additionally, to our knowledge, there are no data on recaptures of turtles which were tagged in the channel and recaptured elsewhere. In essence, we do not have data to define the unit of stock for which the impacts are to be assessed. <u>Because of this fact alone</u>, we cannot make definitive statements about the impact of dredging on a particular turtle stock.

<u>Conclusions of Canaveral Assessment</u>

We have no information on the actual mechanism of mortality by the dredging. Ekberg assumed that all turtles in the channel would be killed by the dredge. We carry forth that assumption to our conclusions; however, we have no validation of this. The above analysis has lead to the following list of conclusions pertaining to turtles in the Cape Canaveral Area:

1) We have no data with which to define the unit of loggerhead turtle stock which might be affected by dredging; therefore, we can make no assessment of the impact of dredging on a particular stock,

2) Assuming a trawl efficiency of 46%, the estimated numbers of loggerhead turtles in the Ship Channel at any one time is 415 (1 juvenile; 309 sub-adults; 105 adults),

3) Assuming that the alternative parameter sets of Table 3, are reasonable estimates, that the age distribution of loggerheads is stable, and that mortality rates do not increase with age, then using the survival projection curve we estimate that the breeding females of the Cape Canaveral Area can produce a population of from 13,703 to 165,371 juveniles; from 715 to 68,313 sub-adults; from 4200 to 9000 adults; and from 4915 to 64,443 adults and sub-adults, together.

4) Given the above and 100% mortality of turtles in the channel by dredging, then it is expected that the mortality of juveniles will be from 0.0006% to 0.007% of the-population of juveniles generated by the Canaveral breeding females; sub-adult mortality will be from 0.45% to 43.22%; adult mortality will be from 1.17% to 2.5%; adult and sub-adult mortality combined will be from 0.64% to 8.42%. Note again, that there has been no demonstrated relationship in a population sense between the channel turtle and the breeding females of the Canaveral area. Since we cannot choose between the parameter values of the model; i.e., we have no data with which to show if some parameters are erroneous estimates, then the above percents are equally reasonable and we cannot choose a most likely outcome within the ranges,

5) Dredging in the channel at sampling sites 1 through 5 (see Table 1) should produce no impact on turtles; as the number encountered at these sites is extremely small

6) The Atlantic Ridley (an Endangered Species) occurs in the channel with an overage abundance of 0.5, i.e., one Ridley resides in the channel on the average of every other sampling period. Presumably, these turtles would also be subject to dredging mortality.

Future Research Needs

The foregoing has shown what data are needed for comprehensive turtle population analysis. We must analyze these needs in terms of two objectives: 1) increasing our understanding of turtle populations in the Canaveral Area, and 2) being able to transfer the knowledge to problems at other sites. The emphasis of research efforts will depend on the choice between (or mix of) objectives.

Nancy Thompson, of my staff, has assessed the data needs for general turtle population analysis in light of data that is available or commonly collected (see attached report). In particular, the data gaps she notes as being crucial are lack of definition of turtle stocks and description of the survival curve. The present analysis has underscored her conclusions.

Comments have been made previously in this memo on the suitability of the survival projection model versus more direct estimates of the survival curve (age-distribution). It would seem that direct methods will provide more precise estimates. However, considerable analysis will have to be done to design sampling schemes such that each location or time is properly represented in the sample. This could be implemented for the Cape Canaveral Area to learn more about this "population" or more diversified areas may be picked. The choice depends on the objective.

The stock definition problem might be somewhat improved by tagging turtles elsewhere than in the channel, to see where they might move. Also, recoveries of animals tagged in the channel (via stranding networks) might provide information. However, these results will be slow in coming to fruition. Comprehensive coordinated programs are needed to pass information between researchers which will help in stock definition.

The trawl sampling method can be an effective tool for producing density estimates. This will be especially so if the efficiency of the trawl can be stratified by the relevant factors which affect it. This is extremely important, because well defined efficiency corrections will allow trawl samples to be used outside the channel and at other locations to produce density estimates. Then with properly designed sampling plans, these might be converted to excellent population indices or actual abundance estimates. Otherwise, it seems the only feasibile method for estimating density or abundance of non-beached turtles is by aerial survey; and this technique needs further experimentation on estimating turtle surface times before true abundance can be obtained.

The present objective of monitoring density within the Canaveral Channel using the trawlers could probably be improved somewhat by proportionally allocating the effort between sampling sites (see Table 1). The low density sites should not be sampled as frequently. Additionally, the entire width of the channel should be represented in the sample. These modifications are specific to research at the Canaveral location. However, their implementation should be achievable with no additional effort.

Finally, we must look at the opportunity for research, if the dredging does take place. This could be a unique opportunity. If possible, the actual numbers that are killed should be obtained (possibly to be obtained by an observer(s)) and the carcasses collected, if that is feasible. Secondly, we should continue to monitor before and after the dredging. From this we can estimate the magnitude of the mortality, but more importantly we can get the rate of migration back into the channel after it is depleted. These rates may be illuminating as to the migration patterns of turtles in general, not specifically at Cape Canaveral. If some tagging effort could be expended outside of the channel, we might be able to determine the source of turtles entering the channel. Sampling effort should be increased immediately after the dredging in order to detect these changes. Perhaps alternative sources of funding could be developed for this extended effort (Corps. of Engineers?).

In conclusion, the data needs for precise turtle population analyses are critical, particularly in stock definition and abundance estimates by age group. The analysis herein, although far from definitive, has helped to provide a focus for future research efforts.

cc: W. Fox w/attachments
F. Berry w/attachments
W. Richards w/attachments
A. Kemmerer w/attachments
N. Thompson w/attachments
R. Conser w/attachments

UNITED STATES DEPARTMENT OF COMMERCE
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February 7, 1980

TO: FILE

FROM: D. R. Ekberg, F/SER6 Don Ekberg.

SUBJECT: Loggerhead Sea Turtles in the Cape Canaveral Area

In a letter to Mr. James L. Garland, Chief, Engineering Division, Jacksonville District, Department of the Army, Corps of Engineers, on January 22, 1980, the Fisheries Assistant Administrator, Terry L. Leitzell, stated "We issued a biological opinion on a previous consultation request for this area on March 30, 1979. Based on the results of that threshold examination, ~~and on new data gathered~~ in the interim, I am of the opinion that dredging may result in the loss of large numbers of loggerhead sea turtles, but is not likely to result in jeopardizing either the loggerhead or Atlantic ridley sea turtle stocks." This decision by Mr. Leitzell apparently was based on lack of information from the Southeast Region pertaining to sea turtle populations in the Cape Canaveral area. We had not demonstrated adequately to the Washington office that the Cape Canaveral group of turtles was a sub-species or a distinct population segment of loggerheads in that area. Even though the Cape Canaveral Channel probably has the most dense concentration of loggerhead sea turtles in the United States, and in spite of the Regional Office recommendation of jeopardy, the Washington office was not convinced that dredging this channel would have a jeopardizing effect on these turtles.

Data pertinent to the Cape Canaveral sea turtle population have been gathered from shrimp trawl captures and surface observations in the channel, estimates of nesting females in the Cape Canaveral area, tagging data from nesting females and observations of the number of eggs laid by nesting females (see references). These data are summarized in Table 1. The nesting females in the Cape Canaveral area are estimated at 850 which is approximately 10% of the total Florida nesting females. Assuming that only 40% of the adult females nest on a yearly basis, the total adult female population in the Cape Canaveral area is estimated at 2125, and, assuming a one-to-one sex ratio of males to females, the total adult loggerhead sea turtle population in the Cape Canaveral area may be estimated at 4250. If each female who nests deposits 100 eggs per nesting and nests 3.2 times per year, the total number of eggs deposited in the Cape Canaveral area by nesting females is 270,000. If it is assumed that only 10% of the eggs survive to hatchlings that enter the sea, 27,000 hatchlings result. Although the age structure of turtles is not known, Figure 1 was constructed based on approximately 10 turtles of age 26 years and slightly less than a thousand turtles at age 8 (which is taken as the age required for sexual maturity). The turtles in the 8 to 26 year class total approximately 4250. Since the mortality of younger turtles is certainly higher than older turtles, the curve for adult turtles and entering hatchlings was fit with a curve of gradually increasing slope as the age of turtles decreased. (Hillestad and Richardson, 1977, have discussed possible slopes for this portion of the curve depending on the fate of juvenile sea turtles.) If the population curve for turtles in Figure 1 is reasonable, then the sub-adults (4 to 8 years old) are estimated at 7,900. Carr and co-workers in 1979 and Berry in 1979 have shown that turtles exist in the Cape Canaveral Channel throughout the year. Observations of turtles in the channel and captures using 75-foot trawls range from about 40 to 200 turtles. If it is assumed that this sampling of turtles is approximately 10% of the total Cape Canaveral Channel population, then the population in the channel may be estimated at 400 to 2,000 turtles. Since the majority of these turtles are subadults, the percentage of the Cape Canaveral population present in the Cape Canaveral Channel may be estimated to be 5 to 25 percent. The dredging of the entire Cape Canaveral Channel could result in the death of up to 2,000 turtles or approximately 25% of the available subadult turtles in Cape Canaveral area.

This rough analysis of the loggerhead sea turtle in the Cape Canavera area certainly can be improved with a better data base. More information is needed on sex ratio, hatchling survival and other population dynamics. However, in view of the available data, it appears that dredging the Cape Canaveral Channel should be considered as placing an already threatened species in further jeopardy. If the population trend in loggerhead sea turtles is downward, and this must be the case if the turtles are consider to be threatened, then destroying several hundred turtles can only hasten the time to extinction.

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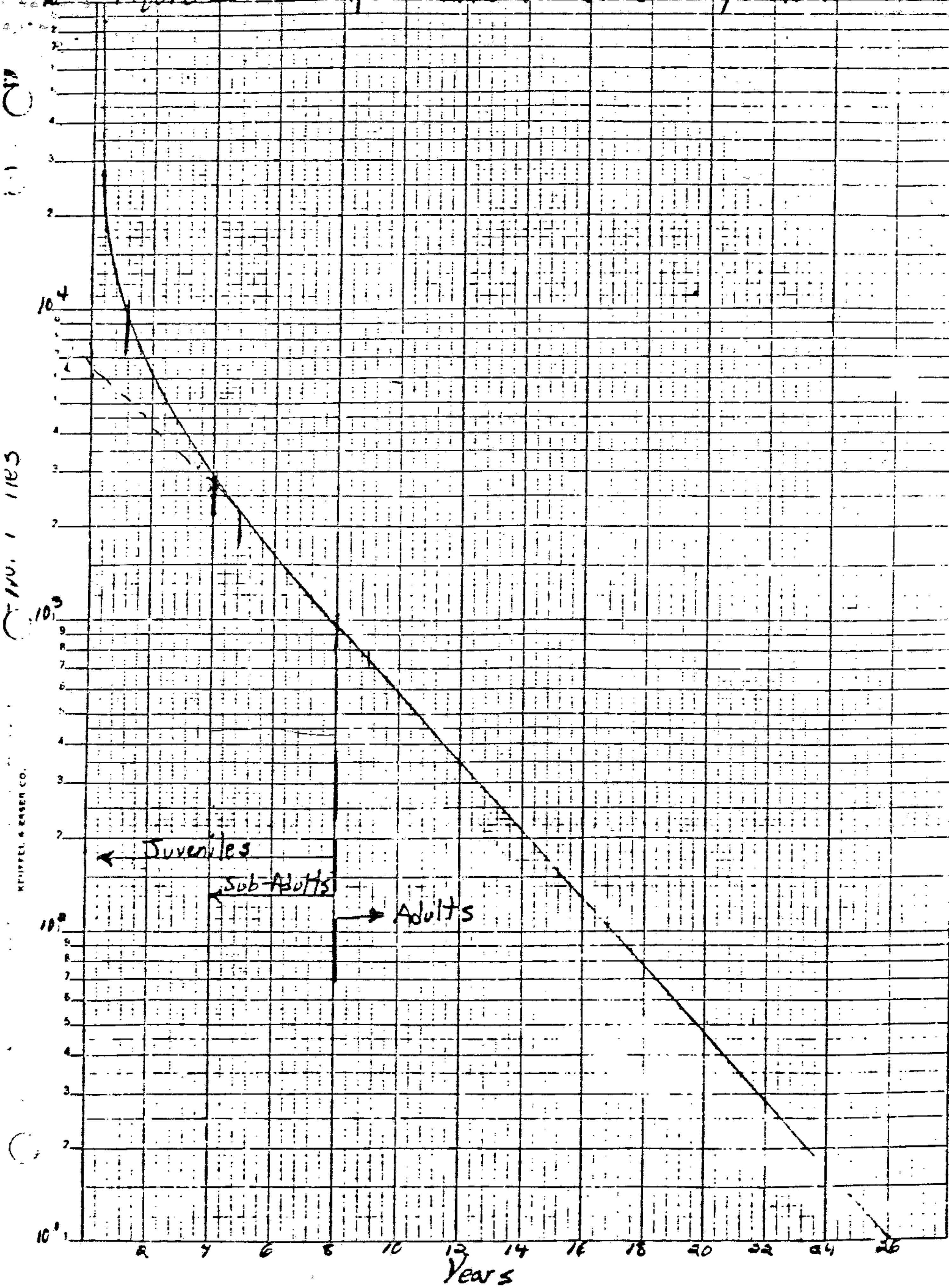
TABLE 1. LOGGERHEAD SEA TURTLE POPULATIONS

	Cape Canaveral	Florida	SE USA
Nesting Females [1,2]	850	8,000	10,000
Total Adult Females [1,2] (40% of adult females nest)	2,125	20,000	25,000
Total Adult Males (1:1 sex ratio)	2,125	20,000	25,000
Total Adults	4,250	40,000	50,000
Eggs Layed [1,2] (3.2 nestings/♀ 100 eggs/nesting)	270,000	2,560,000	3,200,000
Hatchlings [1] (10% survival)	27,000	256,000	320,000
Sub-Adults (4-8 years old) See Figure 1. (Cape Can Area)	7,900		
Cape Canaveral Channel Population (See Text)	400-2000		
% Sub-Adults in Channel	5-25		

Figure 1   Cape Canaveral Turtle Population



SURVIVAL PROJECTION MODEL
by
Ramon J. Conser

N_{HM_A} = number of hatchlings given adult mortility is equal to that of juveniles and sub-adults.
N_A = number of adults
N_{A1} = number of turtles entering adult group
M_A = instantaneous mortality rate of adults
t_{A1} = age at which turtles reach adulthood
t_{max} = maximum age of turtles
N_{min} = number of turtles left at maximum age
N_{SA1} = number of turtles entering sub-adult group
t_{SA1} = age at which turtles enter sub-adult group
M_{SA} = instantaneous mortality rate of sub-adults
N_{SA} = number of sub-adults
N_H = number of hatchlings entering water
N_J = number of juveniles
M_J = instantaneous mortality rate of juveniles

Using the above notation and the following formulae, N_J, N_{SA} and the mortality rates (M_J, M_{SA}, and M_A) can be calculated.

$$N_A = N_{HM_A} \int_{t_{A1}}^{t_{max}} e^{-M_A t} \, dt$$

$$N_A = N_{A1} \, e^{M_A t_{A1}} \int_{t_{A1}}^{t_{max}} e^{-M_A t} \, dt$$

$$N_A = \frac{N_{A1} \, e^{M_A t_{A1}}}{-M_A} \left[e^{-M_A t_{max}} - e^{-M_A t_{A1}} \right]$$

$$N_A = \frac{N_{A1}}{M_A} \left[1 - e^{-M_A (t_{max} - t_{A1})} \right]$$

$$\frac{1}{N_{A1}} = \frac{1 - e^{-M_A (t_{max} - t_{A1})}}{M_A \; N_A}$$

$$N_{A1} = \frac{M_A \; N_A}{1 - e^{-M_A (t_{max} - t_{A1})}} \qquad (1)$$

If $N_A = N_{min}$ at t_{max} then

$$N_{A1} e^{-M_A (t_{max} - t_{A1})} = N_{min}$$

$$N_{A1} = N_{min} e^{M_A (t_{max} - t_{A1})} \qquad (2)$$

From (1) and (2) we have

$$\frac{M_A N_A}{1 - e^{-M_A (t_{max} - t_{A1})}} = N_{min} e^{M_A (t_{max} - t_{A1})}$$

$$M_A N_A = N_{min} \left[e^{M_A (t_{max} - t_{A1})} - 1 \right]$$

$$M_A N_A - N_{min} e^{M_A (t_{max} - t_{A1})} + N_{min} = 0 \qquad (3)$$

N_A, t_{A1}, and t_{max} are known (or assumed) and M_A can be found numerically using Newton's Method from (3) - then N_{A1} can be obtained from (2).

Assuming subadult mortility (M_{SA}) is a function of adult mortality (M_A) such as

$M_{SA} = \gamma M_A$ where γ is a constant, then

$$N_{SA1} = N_{A1} e^{M_{SA} (t_{A1} - t_{SA1})}$$

then

$$N_{SA} = N_{SA1} e^{M_{SA} t_{SA1}} \int_{t_{SA1}}^{t_{A1}} e^{- M_{SA} t} dt$$

$$N_{SA} = \frac{N_{SA1} e^{M_{SA} t_{SA1}}}{- M_{SA}} \left[e^{- M_{SA} t_{A1}} - e^{-M_{SA} t_{SA1}} \right]$$

$$N_{SA} = \frac{N_{SA1}}{M_{SA}} \left[- e^{- M_{SA} (t_{A1} - t_{SA1})} + 1 \right]$$

Then mortality for juveniles (M_J) can be found from

$$N_H \; e^{-M_J \; t_{SA1}} = N_{SA1}$$

$$\ln(N_H) - M_J \; t_{SA1} = \ln \; N_{SA1}$$

$$M_J = \frac{\ln (N_H) - \ln N_{SA1}}{t_{SA1}}$$

Then the number of juveniles (N_J) is

$$N_J = N_H \int_0^{t_{SA1}} e^{-M_J \, t} \, dt$$

$$N_J = \frac{N_H}{-M_J} \left[e^{-M_J \; t_{SA1}} - 1 \right]$$

$$N_J = \frac{N_H}{M_J} \left(1 - e^{-M_J \; t_{SA1}} \right)$$

Newton's Method

$F(M_A)$ is a specified function of the adult mortality rate, i.e.,

$$F(M_A) = M_A N_A - N_{min} e^{M_A (t_{max} - t_{A1})} + N_{min}$$

$$F'(M_A) = N_A - N_{min} (t_{max} - t_{A1}) e^{M_A (t_{max} - t_{A1})}$$

$$M_{A_{n=1}} = M_{A_n} - \frac{F(M_A)}{F'(M_A)} \qquad (4)$$

where n is the interation. Recursion equation (4) is repeated until the solution (M_A) converges.

An Assessment of
Turtle Population Analysis Data Needs

by

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March 25, 1980

Population size estimates are only one of a number of statistics required to fully understand the dynamic properties of a population. In addition rates of numerical change are usually estimated from birth and death rates. However, the usefulness of a set of parameters chosen to analyze a population depends upon their relative ease of estimation, the extent to which they collectively describe the significant properties of a population, ability to extrapolate beyond the data from which they were calculated, the directness of their relationship to population processes and their generality. A choice of parameters is usually the result of a compromise between these criteria. The main parameters for which estimates are usually derived are listed in the outline which is included as an Appendix of this report.

The most conspicuous species in Southeast U.S. waters is the loggerhead, Caretta caretta. This report specifically adresses the data now available for this species and the green turtle, Chelonia mydas. The necessary data required for complete analysis is defined and hopefully this report will offer some direction of efforts which will result in parameter estimates for all marine turtle species.

While the immediate task is to derive realistic estimates for population sizes by area at the present time (i.e. point in time and space estimate), the ultimate goal is population analysis. The cause-effect relationship between all the above parameters often requires concurrent estimation and evaluation.

In this report I will evaluate the status of turtle population analysis in relation to the available data and present data collecting techniques. The outline on population analysis which follows summarizes the information usually desired and/or required for complete population analysis. Each parameter will be discussed in this report. However, because of the inter-relationship between parameters, there is necessary redundancy.

I. Population Definition

Limits

The analysis of a population implies that the population under consideration is defined and bounded. Hence, the first problem is encountered.

Because dispersal patterns and migration routes are unknown for all stages, a marine turtle population is usually temporally bounded within the nesting season and spatially limited to state, beach, island, etc. (whichever is most convenient). Thus, "populations" are considered composed only of female recruits and remigrants. Assuming "enough" males are present, this restriction is no barrier to population analysis. Until there is evidence that refutes a 1:1 sex ratio, the number of adult females will have to be assumed to represent half of the total breeding population.

The breeding season is known for all species in our area from tag-recapture data. Marine turtles demonstrate a birth-pulse type of reproduction and hence nesting in the Southeast U.S. area is not continuous but restricted, in general, to late spring and summer.

It appears likely that sub-adult and adult loggerheads feed as far north as New York waters, and move seasonally in a north/south direction. Hence, for a "population" which is defined to include sub-adults and non-breeding adults, only density estimates may be obtained from pelagic aerial surveys. Seasonal movements may also be determined from pelagic aerial surveys and result in density estimates over time.

II. Population Structure

Age

No reliable method is yet available for aging sea turtles beyond the hatching stage. Sea turtles populations are composed of state classes defined by sizes which are species and perhaps population specific. Differential growth rates presently prohibit the extrapolation of age from size data. Generally, populations are considered to include at least six life history stages. These stages are:

a) egg
b) hatchling
c) yearling
d) juvenile
e) sub-adult
f) adult

A frequency distribution of numbers per stage are derived for eggs, hatchings, and adults from counts. The number of recruits vs. remigrants is derived from tag-recapture data and is generally known and also incorporate corrections for tag loss. It is assumed all nesting females without tags or evidence of previous tagging are recruits. No estimates for the numbers of yearling, juveniles or sub-adults are available. Thus, for any nesting season, numbers of eggs, hatchlings and nesting females are determined.

Sex Ratios

Sex ratio of the egg, hatchling and sub-adult stages are unknown. Currently ratios are determined for adults from trawl catches, and the assumption is made that the probability of capture is equal for males and females. Aerial pelagic surveys MAY be used to determine sex ratios, assuming mature females are at least some predetermined carapace length. Adult males can be identified by the presence of a tail which extends beyond the rear of the shell. However, while we know females do not breed every year, we do not know if males are also periodic participants. Thus, at any given time during the breeding season the number of males sighted may represent all the breeding males for that breeding group. Movements of males are unknown. Whether males return to the same breeding area or not is also not known. However, aerial surveys can be used to derive relative estimates (an index) of adult males and females. While the dynamic properties of a population are primarily dependent upon the number and characteristics of the females, when considering the effect of exploitation, the number of males present is also important. For example, exploitation which focuses on sub-adults, could effect the number of male recruits present in the population for several years because age at sexual maturity is not known. Thus, the lag time for hatchlings to become recruits (generation time) is not known.

III. Abundance

A. Eggs and Hatchlings.

The numbers of eggs deposited in a given year is derived from direct counts or by the product of some mean value for numbers of eggs per nest and the total numbers of nests. The numbers of eggs deposited per female is used to estimate reproductive rate. Tag-recapture studies give estimates of the numbers of nests per female, which multiplied by mean number of eggs per nest gives a fertility value (m_x = reproductive rate).

I know of no other way to derive estimates of numbers of hatchlings other than by on-site counting. Either hatchlings are counted upon emerging from the nest or the number of hatched eggs are totalled. Often when percent hatch is known this value is multiplied by total eggs to give total hatchlings.

Females do not nest every year, rather most nest every 2,3 or 4 years. If the cycle is known for a given "population" or breeding colony the multiplication of the total number of eggs and hatchlings produced in one year times the number of years in a cycle gives a first approximation of the total number of eggs and hatchlings produced in a breeding population for one breeding cycle (i.e. 2,3 or 4 years) of data are available, mean values and variances may be calculated. Note that such estimates for hatchlings are only relevant for the stage prior to individuals entering the water.

B. Nesting Females

A quick estimate of the total numbers of nesting females ($\hat{N}_n$) in a given season is derived by taking the total number of nests and dividing by the average number of nests and dividing by the average number of nests or clutches per female (Fig. 1). In general these data are available by state or nesting beach. Multiplying by the interbreeding cycle (2,3 or 4 years usually) gives a rough estimate of total number of nesting females Numbers can be corrected (weighed) when the interbreeding cycle is enumerated by frequency of individuals/cycle. These data are derived from tag-recapture studies, and are generally available for _Caretta_ _caretta_ (loggerhead) and _Chelonia_ _mydas_ (Atlantic green turtle). Tag recapture studies have also been used to correct for the total number of nests and eggs per clutch per recruit vs. remigrant which may differ significantly by area or year. The information required to correct for recruit vs. remigrant clutches and the numbers of recruits vs. remigrants, are derived from tag-recapture studies. Hence, tag-recapture studies alone give direct estimate of the numbers of total nesting females/year which can be further differentiated into total recruits (individual without tags or evidence of tags) and total remigrants per year (individuals with tags or evidence of tags).

Aerial surveys of nesting beaches are used to determine relative nesting activity through any given season. Utilizing these data for estimation of the total numbers of nesting females presupposes that only those crawls resulting in nests are counted (true crawls). An experimental design for the dates and numbers of flights is a difficult task. All true crawls must be counted and true crawls are generally differentiated from "false" crawls by an additional field effort on the beaches (ground truthing). In areas of high nesting density it is often difficult to separate crawls and counts may be grossly inaccurate. When flights are made to correspond with tidal activity (about every two weeks) to insure only fresh crawls are counted, the data are biased by the probable interesting interval (12-16 days) and the nests of the same females may be counted during each flight. These problems preclude use of present aerial techniques at this time for obtaining relatively accurate estimates of the nesting population size. Again, the aerial effort assumes knowledge of the numbers of clutches per female which are derived from tag-recapture studies.

Because of lack of knowledge on dispersal of sea turtles, single season estimates (of N_n) are only that. Whether loggerheads are site-specific (i.e. return to nest at the same beach within a season or successive season) has not been conclusively demonstrated as has been for green turtles (Chelonia mydas). This will probably be determined with continued tag-recapture studies of loggerheads. Figure 2 summarizes the factors influencing the number of nesting females in a population.

IV. Dispersal and Migration

Caretta caretta is the most conspicuous species in our area. At this time it is not known what immigration and emigration rates are for C. caretta (zero or non-zero). Movements of females are generally from a feeding ground to a nesting beach. Routes of these breeding migrations are not known. Assuming that at this time loggerhead breeding colonies have been saturated with tags that all nesting turtles are encounted and there is no immigration or emigration, then any animal that arrives at a nesting beach without a tag or evidence of tagging is considered a recruit or "neophyte" (first time nester). Hence, the population may be treated as closed and all additions to the breeding population are derived from recruitment.

Probably the only way to define migratory routes and movements of animals offshore will be through observers aboard commercial fishing vessels and pelagic aerial surveys. These appear to be the only ways to determine where animals are spatially distributed by size class and by time.

V. Mortality and Survivorship

Mortality of "eggs" is determined by using percent hatch. Usually a mean value is derived with some measure of variability. Again, sampling is such that percent hatch is considered constant over space, time, female, etc.

Hatching mortality is known only for animals in transit from nest to water and derived from observation (counts). It is assumed that mortality is high until some critical size is attained. A survivorship curve may follow a negative exponential with approximately 1% of the hatchlings successfully breeding at least one time.

Mortality of sub-adults may be derived from catch per unit effort data. However, this statistic presently is derived from the presumed survivorship curves.

VI. Recruitment

Recruitment is estimated by knowing the total stock size. When tag-recapture data are available, the ratio of recruits (animals without tags) to total population size may be calculated. Multiple tag-recapture data are useful in elucidating trends. The effect of year to year fluctuations in recruitment may be a function of population density and/or environmental factors. Whether these factors are additively or multiplicatively synergistic is unknown. Again the problem of associating sub-adults with a given breeding population is a complicating factor.

VII. Conclusions

Table 1 summarizes the primary gaps in our knowledge of marine turtles which are relevant to population analysis. Table 2 summarizes the type of studies which result in computation of population parameters used in population analysis. If a population is not restricted to females, then well-designed pelagic aerial surveys give the best estimates of total numbers, generally without differentiating by sex. Thus a biomass estimate is derived, bounded by some visibly minimum size class. Figure 3 summarizes the possible decision making process to determine the neccessity of pelagic aerial surveys. At present there is no information on dive times in turtles. Estimates derived from present pelagic survey techniques need to be supplemented with research on surface and diving times, without which the density estimates so obtained probably represent minimum numbers.

In summary, the data on hand for sea turtles includes:

1. Number of eggs deposited each season per female (m_x).
2. Percent hatch (i.e. egg to hatchling survivorship).
3. Number of nesting females per season.
4. Interbreeding cycle and numbers of females per cycle (usually 2,3 or 4 years).
5. Estimates of recruitment (no tags vs. tags, corrected for tag loss).

Given these data and resulting parameter estimates (i.e. statistics), partial population analysis can be completed at this time. We know that for a female to replace herself, one female hatchling must survive to breed. Given a 1:1 sex ratio of hatchlings, the value of survivorship from hatchling to recruit (p_1) is approximately .01 (1 in 100) for replacement.

From several years of tag-recapture data we have already estimated recruit to remigrant survivorship (p_2). However, we cannot partition total mortality into natural vs. "other", for remigrants. If we assume turtles represent a stable age (stage) distribution and $p_1 = .01$, if the breeding population is numerically declining than $p_1 < .01$. Both possibilities can be examined and used to derive a <u>relative</u> estimate of mortality due to fishing.

Another way to investigate a marine turtle population with existing data on nesting females and fertility rates is to begin by assuming some range in age of sexual maturity and working backwards. That is, complete a cohort analysis in reverse. If incidental catch data are available, then this reverse cohort analysis can incorporate an estimate of fishing mortality. The choice of age of sexual maturity at this time is a representative range (e.g. 6-13 years for *Chelonia mydas*). Because this age represents generation time, this age determines recruitment rate and hence will effect the estimate of numbers of sub-adults in the "population".

Table 1 summarizes the primary discontinuties in data preventing complete population analysis. Note for both above suggested methods certain assumptions must be made. When more data are available, through iteration more accurate estimates of numbers and rates will be derived.

Where do these "more data" come from? Table 1 lists the major unresolved problems which prohibit elimination of the several assumptions which must be made for population analysis (i.e. sex ratio; age of sexual maturity; site specificity, etc.). It appears likely that continued tag-recapture efforts will solve (for breeding females) the second 2 problems (in part or whole). Scientific observers aboard commercial fishing vessels could improve these data considerably. Assuming that scientific trawling is impractical (i.e. not cost effective), then tag-recapture studies can be supplemented with well-designed pelagic aerial effort, stratified by place and time given an expected distribution of the animals. Again, estimates of abundance are conservative because bottom time versus surface time of marine turtles is not presently known. The decision to complete aerial surveys to determine population limits, numbers, distributions and movements is summarized in Figure 3.

The intent of this report is to identify data needs directed towards population analysis. While incomplete data exist, partial analysis is possible now given the data on hand. Immediate efforts should be directed to a) defining populations and b) determining the shape of the survivorship curve.

Fig. 1 .The following scheme summarizes how $\hat{N}_n$ (the number of nesting females) can be derived from currently available data. Assuming a 1:1 sex ratio, $2\hat{N}_n$ gives the number of breeding turtles($\hat{N}$).

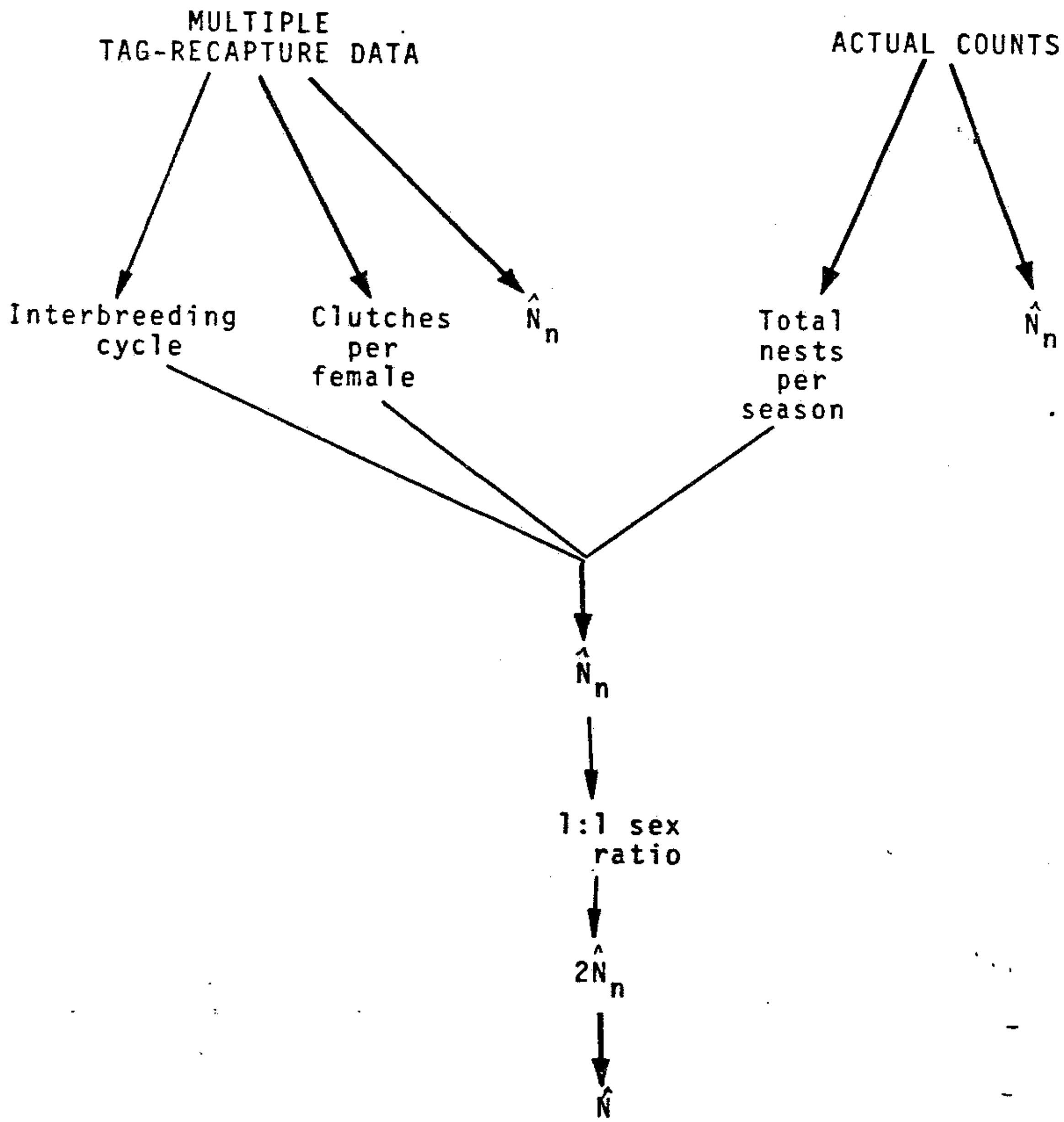


Fig. 2 Major factors influencing size of breeding or nesting population or "sub-populations". All factors but mortality estimates for the sub-adult stages can be determined from data on hand.

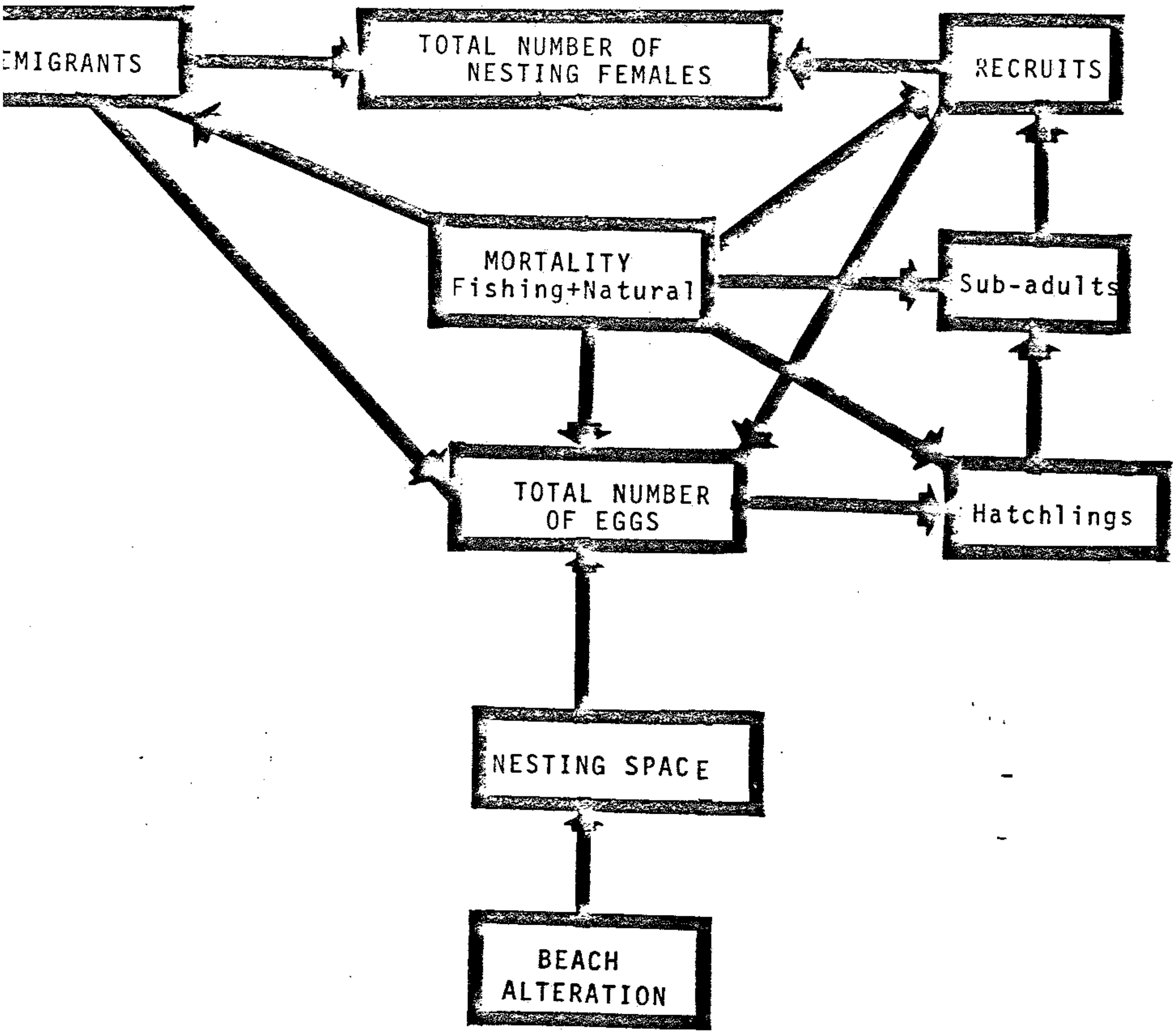


Table 1 Primary Unresolved Problems Relevant to Turtle Population Analysis:

1. Defining the population spatially and temporally for each or all stages.

2. Determining migration routes and dispersal patterns of both sexes, for all stages.

3. Effect of population density and environmental alteration on the dynamic properties of the population.

4. Sex ratio for all stages.

5. Lack of data on sub-adult stage including age-growth data and age of sexual maturity; both relevant to determination of actual sub-adult survivorship.

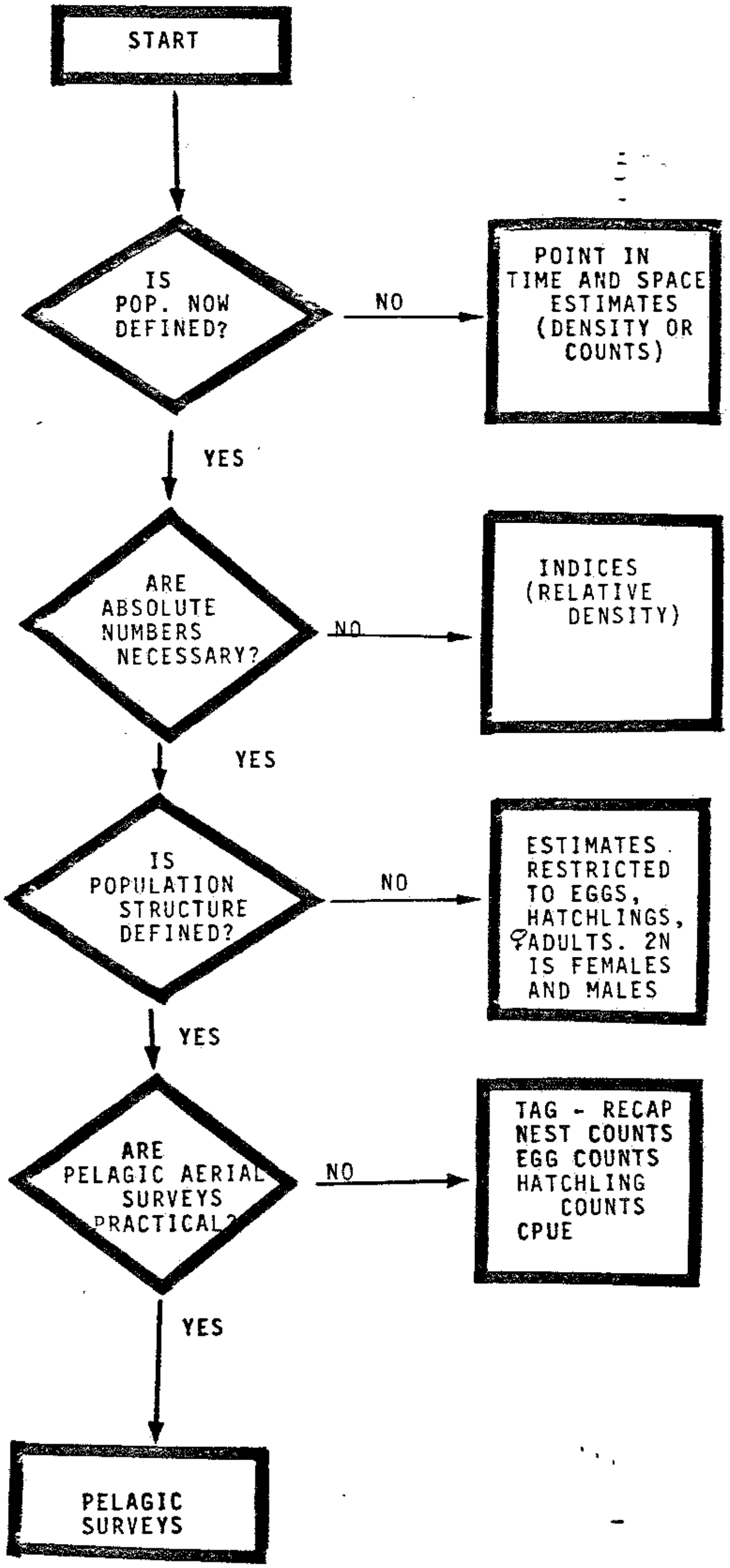
Table 2 Summary of information resulting from field efforts.

DATA SOURCE	AVAILABILITY	RESULTS
I. TAG-RECAP STUDIES	1. yes*	1. Estimate of $\hat{N}_n$
	2. yes	2. Estimate of adult survivorship
	3. yes	3. Recruitment rate
	4. yes	4. Point to point movements
	5. yes	5. Growth of adults
	6. yes	6. Reproductive rates
II. CATCH DATA	1. no**	1. Population structure
	2. no	2. Estimate of fishing mortality, F by size class
(catch composition and cpue)	3. yes	3. Distributions of turtles relative to fishing effort
	4. yes	4. $\hat{N}_h$
III. GROUND COUNTS	1. yes	1. Index of nesting activity
	2. yes	2. Relative nesting density
	3. yes	3. Egg survivorship, $\hat{N}_e$
	4. yes	4. Hatchling survivorship from nest to water, N_h
IV. AERIAL SURVEYS	1. no	1. Estimates of density $(\hat{D})$
	2. no	2. Population boundaries (i.e. distributions by species, size class, time, space)
	3. no	3. Movements and migratory routes
	4. no	4. Estimate of total population size (i.e. bounded by minimum carapace size class)

*yes indicates that data are now available

**no indicates that data are not present and further research effort is needed

Fig. 3 Decision tree to determine the necessity of pelagic aerial surveys.



APPENDIX

An Outline of Parameters commonly Estimated in Population Analysis

Population Analysis

I. The Population
    A. Limits
    B. Breeding system
    C. Parameter choice
        1. age specific survival
        2. age specific fertility, fecundity
        3. frequency distribution by age
        4. sex ratio
        5. numbers or density estimates
        6. correlate statistics
            a. birth rate
            b. death rate
            c. rate of numerical change

II. Age
    A. Structure
    B. Distribution

III. Abundance
    A. Indices (relative density)
    B. Absolute density
        a. total counts (censuses)
        b. guesses
        c. sampled counts
        d. selective additions-removals
        e. non-selective additions-removals
        f. corrected or weighted indices

IV. Dispersal and Migration

A. Patterns

B. Pattern detection

C. Effect on parameter estimation

V. Fecundity

A. Season of births

B. Frequency of births

C. Sex ratio

VI. Mortality

A. Patterns

1. selective removals
2. non-selective removals
3. seasonality

B. Partitioning

1. natural
2. fishing

VII. Recruitment

A. Dependence on density of adult population

B. Estimation of rates

VIII. Relationship between parameters

A. Rates of increase or decrease

1. finite
   a. realized
   b. potential

2. instantaneous
   a. realized
   b. potential

VIII. Relationship between parameters (cont.)

B. Evaluation of demographic vigor

1. stability of parametal relationships
2. stability of population size
3. stability of population structure

a. interpretation of age distribution