ROLE OF A NEMATODE IN NATURAL MORTALITY OF SPOTTED DOLPHINS

Parasitism was advanced by Delyamure (1955) as a major factor in the natural mortality of cetaceans, and infestation by helminths was implicated strongly as the cause of death in some stranded common dolphins (*Delphinus delphis*) (Ridgway and Dailey 1972). Severe and irreversible lesions of the skull of dolphins (*Stenella* spp.) caused by a nematode (*Crassicauda* sp.) were more prevalent among young animals than among old animals (Dailey and Perrin 1973). The reduced frequency of lesions with age indicated that severely infected animals were dying of the parasitic infection or a related cause (Dailey and Perrin 1973). We report quantification of mortality related to *Crassicauda* sp. in spotted dolphins (*Stenella attenuata*) in the eastern tropical Pacific.

METHODS AND MATERIALS

The skulls of 704 spotted dolphins were examined for lesions (Table 1). This represented a stratified random sample of dolphins of this species killed incidentally in the purse-seine fishery for tuna in the eastern tropical Pacific Ocean (Perrin 1968). Dailey and Perrin (1973) examined 126 specimens and classified them to age by using growth layers in dentin as an index. The infection rate that they reported was used to develop a stratified random sampling procedure for our study. The number of dolphins with 3 or fewer dentinal layers needed to achieve a coefficient of variation of 0.25 for the estimate of infection rate was calculated. Similarly, the number with >3 layers needed for a coefficient of variation of 0.50 was calculated. The 126 dolphins previously aged were apportioned into these strata. Additional dolphins were selected at sea, on the basis of body length, to achieve the sample size of 704.

The heads were cleaned and examined, and morphometric and sutural data used in age estimation were recorded. The extent of nematode-related damage on the underside of the skull was classified as none, some, or severe (≥2 extensive lesions).

Three methods were used to deter-

mine relative age of the dolphins. First, for the original sample of 126, the actual number of layers was determined from examination of teeth. Second, for the remaining dolphins less than 150 cm long, the number of layers was estimated on the basis of length, using the model of Perrin et al. (1976). Finally, for the remaining dolphins >150 cm long, a regression model was fitted, in which layers were estimated from total length and data on sutural closure for the skulls. The model was

$$Y = e^{b_0} \prod_{i=1}^{8} X_i^{b_i}$$

where Y = number of dentinal layers, and the variables (X) are based on morphometrics and sutural features of the skull. The model was fitted using a multiple linear regression after a logarithmic transformation.

Mortality and infection rates were calculated using the exponential model $N_t = N_0\exp[(r - m)t]$, or $N_t = N_0\exp(a + zt)$, where N_t = % of skulls with lesions at dentinal layer t, N_0 = % with lesions at initial age $t = 0$, m = exponential rate of parasite-related mortality, r = exponential rate of parasite infection, $z = r - m$ = net exponential rate of change in lesion frequency, and $a = \ln(N_0)$. Estimates of the parameters z and N_0, along with standard errors, were calculated using weighted regression formulas after a ln transformation (Steel and Torrie 1960:2181). Standard errors for the parameters were calculated as in Steel and Torrie (1960).

Because we have no data other than frequency of lesions, we cannot partition z into its components of infection and mortality. However, if we assume that past some age at which there is a peak frequency of lesions no significant new lesions occur, then after that age the net change z is equal to the mortality rate m. The same assumption may be made for young animals, such that $z = r$, if no significant mortality occurs during this time. However, the latter assumption possibly is unjustified. Another assumption basic to these analyses is that infection does not affect the likelihood of capture of the dolphins; i.e., an infected dolphin is not more likely to be killed incidentally in the tuna fishery than is an uninfected one.

Table 1. Lesion rate in spotted dolphin skulls, males and females combined.

Age (layers)	Skulls examined (N)	Skulls with lesions	
		N	%
1	68	2	3
2	31	4	13
3	41	6	15
4	21	1	5
5	15	4	27
6	18	4	22
7	18	2	11
8	37	2	5
9	60	5	8
10	63	5	8
11	79	5	6
12	88	10	11
13	82	1	1
14	38	2	5
15	20	1	5
16–19	25	1	4

RESULTS

The parameters of net change in skull lesions for animals with 8 or more dentinal layers were $\hat{z} = -0.1308$, $SE_{\hat{z}} = 0.2940$, $\hat{a} = -2.4563$, and $SE_{\hat{a}} = 0.2081$. When $\hat{z} = -0.1308$, there is a reduction in frequency of lesions of 12.3% per layer (range of 1 SE truncated at zero is 0–34.6%). The maximum frequency of occurrence of lesions is 8.6% of the population (7.0–10.6%) at 8 layers.

Assuming there is no new infection in adults, the mortality rate of infected animals from parasite-related causes is

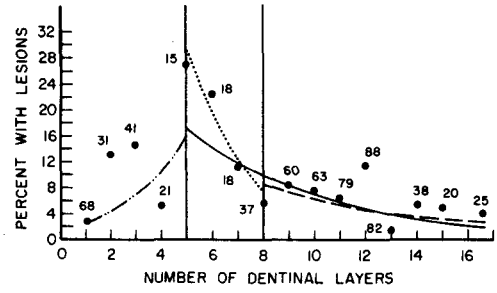

Fig. 1. Relative frequency of spotted dolphin skulls with nematode lesions vs. age in dentinal layers. Numbers are the numbers of skulls examined. Curves were fitted separately for ages (layers) 1–5, 5–8, 5–19, and 8–19.

12.3% per layer. Given that only 8.6% of the population at 8 layers is infected, the mortality rate for the population is 1.1% (0.0858 × 12.3%) with an SE range of 0–3.7%.

The decrease in animals with lesions was 36.0% per layer for dolphins with 5–7 layers. This implies that the lesion-related mortality rate for all animals of this age was 10.6% (0–43.9%). This does not differ from the rate for the older animals (8 or more layers), because of a large standard error resulting from a total frequency of only 10 lesions in the 5- to 7-layer category. Only 51 animals with 5–7 layers were in the sample, and the 7 of these directly aged had no lesions. Therefore, the standard error of the mortality rate was large. However, it is not unreasonable to assume that the mortality rate decreases with age. A more precise estimate may be made by grouping age strata. Grouping all animals with 5 or more dentinal layers, the rate of decrease in spotted dolphins with lesions was 15.5%. The mortality rate for all animals with 5 or more dentinal layers was 2.6% (0–6.2%).

The net infection rate, as exemplified by the presence of lesions, was calculated in a similar fashion using frequencies from animals with 5 or fewer layers. The rate of increase in lesions is estimated to be 53.9% per layer. The fitted rates with the grouped data are presented in Fig. 1.

DISCUSSION

The net infection rate by the nematode that results in lesions in young animals approximates 50% per layer. Then there is a period of reduction in parasite-correlated mortality of approximately 10% per layer for layers 5 through 7. After 8 layers are achieved, the rate of lesion-related mortality drops to approximately 1%.

Whatever the proximate cause of mortality (brain damage, increased susceptibility to predation, etc.), the ultimate cause may be the nematode parasite itself. Future studies of *Crassicauda* sp. in spotted dolphins should include a search for brain histopathology associated with bone lesions. Also required are the specific identity of the parasite and elucidation of its life history. Although related spirurid nematodes use intermediate hosts, potential transplacental transmission or transmission via milk to the nursing calf should be investigated. A closely related form (or even possibly the same form), may cause reproductive failure in Atlantic white-sided dolphins (*Lagenorhynchus acutus*) (Geraci et al. 1978) through invasion of mammary glands.

Estimates of natural mortality of the spotted dolphin in the eastern tropical Pacific range from 7 to 9% per year (Southwest Fish. Cent. Adm. Rep. LJ-76-29, 1976). Estimates of total mortality in 1975 were 10–13% per year. If dentinal layer deposition occurs at 1 layer per year, the rounded-off estimates of nematode-induced annual mortality are 1% per year for animals with 8 or more dentinal layers, and 3% per year for those with more than 5 layers. Higher rates of layer deposition (e.g., 2 per year) would mean

even higher rates of parasite-related annual mortality. These estimates represent 11–14% of the natural mortality of the population, and support the concept that parasitism constitutes a major factor in natural mortality of small cetaceans.

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