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COMPARISON OF LENGTH-FREQUENCY ANALYSES FOR ESTIMATION OF GROWTH PARAMETERS FOR A POPULATION OF GREEN TURTLES

KAREN A. BJORNDAL[1] AND ALAN B. BOLTEN[2]

[1]*Center for Sea Turtle Research and Department of Zoology, University of Florida, Gainesville, FL 32611, USA*
[2]*Center for Sea Turtle Research and Department of Wildlife and Range Sciences, University of Florida, Gainesville, FL 32611, USA*

ABSTRACT: We compared the ability of four length-frequency analysis programs to generate accurate von Bertalanffy growth parameters for a population of green turtles (*Chelonia mydas*) of known growth rates. The four programs were ELEFAN I, Shepherd's length composition analysis (SLCA), projection matrix method, and MULTIFAN. ELEFAN failed to identify a set of parameters that qualified as a best fit. The parameter estimates generated by SLCA successfully described six of the 10 length distributions from the population of green turtles. The parameter estimates produced by the projection matrix method failed to describe adequately any of the 10 length distributions. MULTIFAN generated a set of growth parameter estimates that successfully described all of the 10 length distributions. Although MULTIFAN had the best performance, it requires substantially more initial information and estimates than do the other programs. The best approach—particularly with a poorly studied population—may be to conduct initial analyses with SLCA, followed by analyses with MULTIFAN. Length-frequency analysis is a useful method for the study of growth in populations of immature sea turtles. Further study is required to determine whether these methods are appropriate for populations of sea turtles that include mature individuals.

Key words: *Chelonia mydas*; Demography; Growth; Length-frequency analysis; Sea turtles

INDIVIDUAL growth rate in a population is a critical demographic parameter for understanding the life history of a species and for developing management plans for wild populations. Although growth studies based on mark and recapture of individual animals yield direct measures of growth rates, there are disadvantages to this approach. Mark and recapture studies can be very long term, labor-intensive efforts that require considerable investments of time and funds. The animal may be affected by the mark or tag, so that the measured growth rate is biased. Some species, or some life stages of certain species, are not good subjects for mark and recapture studies because appropriate marking technology is not available or because the probability of recapture of a marked individual is very low. Bias in measurements taken by different observers may introduce an important source of variation.

Sea turtles have a number of characteristics that make them relatively poor candidates for mark and recapture growth studies. Sea turtles are slow growing, so mark and recapture studies are of necessity long term. The probability of recapture of marked individuals is low in many populations because of the characteristics of the life stage (e.g., post-hatchlings in a pelagic habitat), high natural mortality in young life stages, and high human-induced mortality in juvenile and adult life stages. Growth models based on mark and recapture studies have been generated for several populations of a few species of sea turtles (e.g., Balazs, 1982; Bjorndal and Bolten, 1988; Boulon and Frazer, 1990; Frazer and Ehrhart, 1985; Limpus, 1992). However, to generate the regional management plans required to ensure the survival of these species, estimates of growth rates are needed for more species of sea turtles and for more populations within each species.

Length-frequency analysis, in which estimates of von Bertalanffy growth parameters are generated from length distributions of sample populations, have been applied to populations of commercially important species of fish and invertebrates for many years (Hilborn and Walters, 1992). Length-frequency analysis may be a useful approach to the study of growth in other species. In a recent study (Bjorndal et al., 1995), the growth model generated by the length-frequency analysis program MULTIFAN was compared with the growth model from a mark and recapture study of a population of green turtles (*Chelonia mydas*) in the southern Bahamas. MULTIFAN successfully estimated von Bertalanffy growth parameters for this population.

In the present study, three other length-frequency analysis programs—ELEFAN, Shepherd's length composition analysis (SLCA), and projection matrix—are compared with MULTIFAN and the mark and recapture study for the same population of green turtles. All of these length-frequency analysis programs solve for the set of von Bertalanffy growth parameters that yields the best description of the length distributions. However, because the four length-frequency programs employ different analytical approaches, the ability of each program to generate accurate growth models will vary for species with different life history strategies.

ELEFAN I (*E*lectronic *LE*ngth *F*requency *AN*alysis) first restructures the length distributions by assigning positive values to length classes containing many animals and small or negative values to length classes with few animals (Pauly, 1987). Goodness of fit scores are then calculated by summing the values of the length classes through which each growth curve passes. An accurate growth curve will pass through length classes (or modes) with large numbers of animals and thus will accumulate a high goodness of fit score. The growth curve with the highest score is considered to be the best estimate.

As in ELEFAN, SLCA is based on the goodness of fit of the location of modes expected from a von Bertalanffy growth curve to the observed modes in the length distribution. However, length distributions are not restructured as in ELEFAN, and the goodness of fit criterion in SLCA is similar to that used in time series analysis (complex demodulation) (Shepherd, 1987*a*).

The projection matrix method was first developed as a method for forecasting short term catch-rates based on a combination of a time series of length compositions and estimates of growth parameters (Shepherd, 1987*b*). Rosenberg et al. (1986) adapted the method for estimating growth parameters. In this method, proportions in length classes are projected through time as predicted by a set of growth parameters. Expected length frequencies are generated and compared with a series of observed length frequencies, and an unweighted least squares objective function is used to determine the set of growth parameters that yield the best goodness of fit.

The MULTIFAN method integrates a nonlinear parameter estimation technique and maximum likelihood method to estimate the number of significant age classes in the sample population and the parameters of the von Bertalanffy growth model (Fournier et al., 1990, 1991).

We undertook the present study to determine which length-frequency analysis programs successfully estimate growth parameters for a green turtle population. Identification of appropriate length-frequency analyses would provide a valuable tool in the study of sea turtle demography.

Methods

From 1983 through 1992, immature green turtles were captured over their foraging pastures on the north coast of Great Inagua, Bahamas. Each sampling period was approximately 2 wk, and the month of sampling varied among years. Turtles were measured, marked in the trailing edge of their flippers with identification tags, and released at site of capture. The measurement used in this study is standard straight-line carapace length (SCL) measured from nuchal notch to posterior tip of posterior marginal with anthropometer calipers (GPM model 101) to the nearest 0.1 cm. The study area and methods of capture have been described in previous papers (Bjorndal, 1980; Bjorndal and Bolten, 1988).

The length-frequency programs in this study generated estimates of the parameters of the von Bertalanffy equation, which may be expressed:

$$L_t = L_\infty(1 - e^{-K(t-t0)})$$

where L_t is length at age t, L_∞ is asymptotic length, e is the base of the natural logarithms, K is an intrinsic growth rate variable, and t0 is the nominal time that length is zero.

We calculated mean growth rates for each 5-cm carapace length size class from the mark and recapture data. We calculated the mean time that a green turtle takes to grow through each 5-cm interval and estimated the von Bertalanffy growth parameters using nonlinear regression (SAS PROC NLIN: SAS Institute, 1982).

All of the length-frequency programs have the assumptions that growth is described by a von Bertalanffy growth curve, that samples represent the structure of the population, and that recruitment occurs in seasonal pulses. In addition, the projection matrix method has the assumption that mortality is constant over time and equal for all age classes. The MULTIFAN method has the assumptions that the lengths of animals in each age class are normally distributed around their mean length and that the standard deviations of the actual lengths about the mean length-at-age are a simple function of the mean length-at-age.

MULTIFAN requires that the following parameters be specified: expected number of age classes, expected initial K values, mean length of the mode representing the youngest age class, and standard deviation of a distinct mode. We set initial values for age classes to 6, 7, 8, 9, 10, 11, 12, 13, 14, and 15 yr, and for K to 0.01, 0.05, 0.1, and 0.5. The mean length of youngest age class was set to 27.5 cm (in 1988 sample) and standard deviation of mode width to 1.5 for all initial values of age classes and K. There was a significant trend in standard deviation of length-at-age with increasing length, so this parameter was included in the MULTIFAN model.

ELEFAN, SLCA, and the projection matrix method only require that a range of expected initial K values and a range of expected initial L_∞ values be specified. For these three programs, initial range of K values was 0.01–0.15, and initial range of L_∞ values was 50–200. Ranges were narrowed in successive analyses depending on the results of the previous analysis.

The relative accuracy of the growth models generated by each of the length-frequency programs was assessed as in Terceiro et al. (1992) by comparing the age distributions resulting from the growth parameters generated by each length-frequency program with those from the mark and recapture data using Kolmogorov-Smirnov cumulative distribution tests (Sokal and Rohlf, 1981). Alpha was 0.05. We used an age slice program that employs the von Bertalanffy parameters L_∞, K, and t0 to assign length classes to age classes, to transform the length distributions to age distributions.

The length-frequency analysis programs were obtained from two sources. ELEFAN I, Shepherd's length composition analysis (SLCA), the projection matrix method, and the age slice method were from the Length Frequency Distribution Analysis Package (LFDA version 3.10) produced by Marine Resources Assessment Group Limited with support from the British Overseas Development Administration (Holden and Bravington, 1992). MULTIFAN (version 32 (f)) is produced by Otter Research Ltd., Nanaimo, B.C., Canada (Otter Research Ltd., 1992).

Results

From 1983 through 1992, 964 green turtles were captured. Annual samples varied from 45–152 green turtles. The length distributions of all samples are shown in Fig. 1.

Despite repeated attempts with different ranges of parameters K and L_∞, the ELEFAN method failed to identify a best fit. Even when the ranges were narrowed to 0.02 for K and to 15 for L_∞, multiple maxima were found. The parameter estimates for these multiple maxima varied with each run, and the score function values for the multiple maxima were similar.

Repeated analyses with SLCA also yielded multiple maxima, but each run

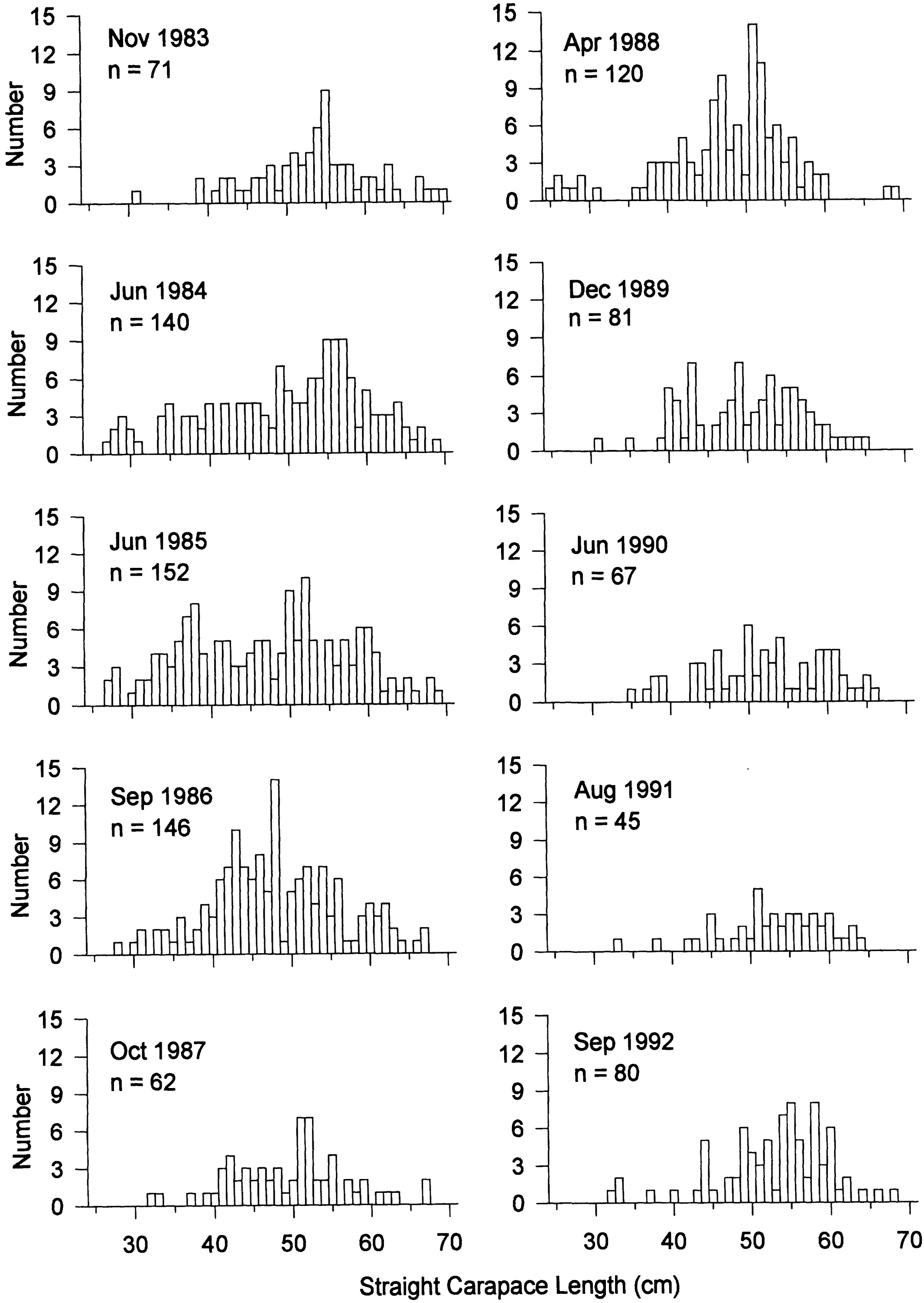

FIG. 1.—Frequency distributions of straight carapace lengths for 10 annual samples from a population of green turtles in the southern Bahamas.

TABLE 1.—Von Bertalanffy growth parameter estimates generated by three length-frequency analysis programs for a population of green turtles in the southern Bahamas. ELEFAN failed to generate a set of parameters.

	K	L_∞	t0
SLCA	0.100	122.79	−0.247
Projection matrix	0.032	82.51	−0.239
MULTIFAN	0.072	99.70	−0.558

consistently identified one maximum that always had a substantially higher score function value than the other maxima that were identified. This set of parameter estimates was used as the best fit generated by SLCA (Table 1).

Successive runs of the projection matrix method led to a range of K from 0.02–0.05 and a range of L_∞ from 80–100. Analysis of these ranges of parameter estimates identified a set of parameters as the best fit (Table 1).

The set of parameters generated by MULTIFAN as the best fit is shown in Table 1. MULTIFAN also identified 12 significant age classes in the population.

The parameter estimates identified as the best fit by SLCA, the projection matrix method, and MULTIFAN were used in the age slice function of the LFDA package to convert the length distributions to age distributions. Results of the comparisons of these age distributions to those generated from the mark and recapture data (Kolmogorov-Smirnov cumulative distribution test) are shown in Table 2.

Six of the 10 age distributions generated from SLCA growth parameter estimates were not significantly different from the age distributions generated from the mark and recapture data. That is, the growth parameter estimates from SLCA successfully described six of the 10 length distributions.

All of the age distributions generated from growth parameters estimated by the projection matrix method differed significantly from those of the mark and recapture study. The projection matrix method failed to describe any of the length distributions.

All of the age distributions generated from the MULTIFAN growth parameter estimates were not significantly different from those from the mark and recapture data. MULTIFAN successfully described all of the 10 length distributions.

TABLE 2.—Comparison of age-frequency distributions generated by each of three length-frequency analysis programs with the age-frequency distributions based on mark and recapture data. Results are not presented for ELEFAN because ELEFAN failed to generate a set of parameters. Values presented are D values from Kolmogorov-Smirnov cumulative distribution tests.

Distribution	SLCA	Projection matrix	MULTIFAN
1983	0.1885	0.8952**	0.1286
1984	0.1837*	0.7556**	0.0709
1985	0.2217**	0.6370**	0.0481
1986	0.1575	0.8190**	0.0548
1987	0.1741	0.8879**	0.1119
1988	0.1273	0.8783**	0.0815
1989	0.1948	0.9131**	0.0610
1990	0.2537*	0.8867**	0.0597
1991	0.2737	0.9487**	0.0445
1992	0.2555*	0.9062**	0.0869

* $P < 0.05$.
** $P < 0.01$.

DISCUSSION

The use of von Bertalanffy growth models in all of the length frequency programs in this study is appropriate for sea turtle populations. In several studies of growth rates of sea turtles, the von Bertalanffy model has been shown to have a better fit than other growth equations (e.g., logistic, Gompertz) to data from populations of wild, immature sea turtles (Bjorndal and Bolten, 1988; Frazer and Ehrhart, 1985; Frazer and Ladner, 1986).

The length frequency analysis programs that were compared in this study varied greatly in their ability to describe accurately growth in the Inagua population of green turtles. ELEFAN could not identify a best fit. Although SLCA also failed to generate a single set of parameters as a best fit, it consistently identified one set of parameters with a substantially higher function score than the other possible fits. This set of von Bertalanffy growth parameters successfully described six of the 10 length distributions. The projection matrix method identified a set of growth parameters, but these parameters yielded age distributions that differed significantly from those based on the mark and recapture data for all 10 length frequencies. The MULTIFAN method had the best performance. MULTIFAN generated a single set of parameter estimates as a best fit, and these parameter estimates successfully described the 10 length frequencies.

Isaac (1990) compared ELEFAN and SLCA with Monte-Carlo simulations of fish populations with different biological characteristics. She found that length distributions of species with slow growth rates were more difficult to analyze because of the multiple maxima of score functions for both ELEFAN and SLCA. However, SLCA performed better than ELEFAN for slow growing, long lived fish, a result that would be expected from the results reported here for the slow growing, long lived green turtle.

Terceiro et al. (1992) reviewed earlier studies on fish and invertebrate species in which ELEFAN and SLCA were compared, and they concluded that SLCA generally performs better than ELEFAN. They went on to compare SLCA and MULTIFAN with simulated length-frequency distributions for fish populations with three, seven and 13 age classes and found that MULTIFAN performed better than SLCA.

In a comparison of SLCA and the projection matrix method, Basson et al. (1988) concluded that the projection matrix method was more robust to variation in length-at-age, and thus the requirement for clearly separated cohorts was less for the projection matrix method than for SLCA. However, because the projection matrix method relies on shifts of the length frequencies along the length axis from sample to sample, this method does not perform well with populations with low K values, and thus small shifts between samples. The poor performance of the projection matrix method with the Inagua population of green turtles probably resulted from the slow growth rates (low K) in that population.

Although MULTIFAN had the best performance of the four length-frequency programs, MULTIFAN also requires much more initial input. MULTIFAN requires the user to provide the expected number of age classes, expected initial K values, mean length of the mode representing the youngest age class, and the standard deviation of a distinct mode. The other programs only require initial ranges of estimates for K and L_∞, although SLCA and ELEFAN are most effective when a narrow range of L_∞ can be set a priori (Basson et al., 1988; Terceiro et al., 1992).

Another difference between MULTIFAN and the other programs is the time required for analyses. MULTIFAN analyses required several hours whereas analyses with the other programs were completed in a few minutes.

A useful approach to initial length-frequency analysis of sea turtle populations—and populations of other species—may be to use SLCA followed by MULTIFAN. Initial exploration with SLCA can be accomplished rapidly. Results obtained from SLCA may then be used as initial estimates in MULTIFAN if the user has no other source of estimates. If SLCA and MULTIFAN generate similar estimates, the user can be more confident of the results.

Just as sea turtles have characteristics that ill-fit them for mark and recapture studies, populations of sea turtles also have characteristics that can make the use of length-frequency analysis problematic. Any factor that acts to obscure modal structure makes length-frequency analysis more difficult. Such factors include long spawning season, variation in individual growth rates that result in variation in length-at-age, cessation or near cessation of growth in old age classes, and high rates of exploitation. If older age classes cannot be distinguished, K will be overestimated and the number of age classes will be underestimated (Terceiro et al., 1992). Also, populations with very high exploitation may have reduced modal structure at the largest sizes, which will result in overestimates of K and underestimates of number of age classes (Terceiro et al., 1992).

The success of length-frequency analysis of the Inagua population of green turtles may be due to the lack of large subadult and adult turtles in this population.

Because growth in length is more rapid in smaller size classes (Bjorndal and Bolten, 1988), the modal structure of the length distributions of the Inagua population is more clear than it would be if the population included adult green turtles.

Caution must be exercised in the application of length-frequency analysis to sea turtle populations. Erroneous results can be generated, as was the case with the projection matrix method in this study. Also, populations that include large individuals and/or that suffer high exploitation by humans—either intentional or incidental—may lack sufficiently clear modal structure to allow successful length-frequency analysis. Length-frequency analysis may yield reliable results only for populations of immature sea turtles.

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RESOURCE PARTITIONING BY THE ESTUARINE TURTLE *MALACLEMYS TERRAPIN*: TROPHIC, SPATIAL, AND TEMPORAL FORAGING CONSTRAINTS

ANTON D. TUCKER[1,2], NANCY N. FITZSIMMONS[1,2], AND J. WHITFIELD GIBBONS[1]

[1]*Savannah River Ecology Laboratory, Drawer E, Aiken, SC 29802, USA*

ABSTRACT: We investigated the foraging ecology of the diamondback terrapin (*Malaclemys terrapin*) in South Carolina by examining fecal samples for evidence of resource partitioning. From 76–79% of the dietary volume was the salt marsh periwinkle (*Littorina irrorata*); crabs (*Uca pugnax, Sesarma reticulatum,* and *Callinectes sapidus*), barnacles (*Balanus*), and clams (*Polynesoda caroliniana*) constituted the remainder. Dietary partitioning is related to the ontogenetic niche of terrapins. Sexual dimorphism occurs in terrapins with females having larger heads and bodies than males. Terrapins with large head widths ingest significantly larger periwinkles and a wider diversity of prey than terrapins with small head widths. Dietary overlap between males and females is greatest when females are small and decreases as females develop larger enlarged heads. Sexual dimorphism in terrapin trophic structures appears to be partially driven by ecological divergence through resource partitioning.

High tides permit terrapins to forage aquatically in upper reaches of the salt marsh. Prey size and distribution are variable and changing tidal heights affect the spatiotemporal availability of prey to foraging terrapins. Divergent foraging strategies for terrapins of different head widths may result in habitat partitioning. Food accessibility rather than food abundance may be a limiting factor for terrapins in areas of high tidal variability. Terrapins are clearly prominent but unrecognized macroconsumers in salt marsh ecosystems.

Key words: Resource partitioning; Turtle; *Malaclemys*; Dimorphism; Salt marsh; Foraging ecology; *Littorina*; Trophic structure

THE diamondback terrapin (*Malaclemys terrapin*) is a common reptile in salt marshes of the southeastern United States (Carr, 1952). Despite having a latitudinal distribution that extends from Massachusetts to Texas (Ernst and Barbour, 1989), their functional role as predators in salt marsh ecosystems is poorly known (Adam, 1990; Day et al., 1989; Pomeroy and Wiegert, 1981). In captivity, terrapins readily consume snails, shellfish, fish, crustaceans, and beef (Allen and Littleford, 1955; Carr, 1952; Coker, 1906, 1920; Davenport et al., 1992; Hildebrand, 1929; Hildebrand and Hatsel, 1926), but dietary studies of wild terrapins are limited to descriptive or anecdotal accounts. Items recorded for the terrapin's diet include snails (*Littorina irrorata, Melampus lineatus*), small crabs (*Gelasimus, Uca*), marine annelids (*Nereis irratabilis*), mussels (*Mytilus edulis*), clams (*Anomalocardia cuneimens*), captured or scavenged fish (*Menidia menidia*), and plant material (*Sargassum*, unidentified

[2] PRESENT ADDRESS: Department of Zoology, University of Queensland, Brisbane 4072, Australia.