Age, growth and population dynamics of tropical squid and sepioid populations in waters off Townsville, North Queensland, Australia

Thesis submitted by

George David JACKSON BSc(Hons) (JCU)

in February 1991

for the degree of Doctor of Philosophy in

the Department of Marine Biology

James Cook University of North Queensland

To Christine, who was a continual
source of encouragement and support
throughout this study.

Frontispiece: The near-shore loliginid squid
Loliolus noctiluca

"Very little is known about the longevity of squids...some of the smaller species might live for four years. It is almost certain that some of the large specimens of giant squids which have been taken were a good deal older than this. But how old nobody knows".

F.W. Lane *Kingdom of the Octopus*, 1974.

I, the undersigned, the author of this thesis, understand that James Cook University of North Queensland will make it available for use within the University Library and, by microfilm or other photographic means, allow access to users in other approved libraries. All users consulting this thesis will have to sign the following statement:

> "In consulting this thesis I agree not to copy or closely paraphrase it in whole or in part without the written consent of the author; and to make proper written acknowledgment for any assistance which I have obtained from it."

Beyond this, I do not wish to place any restriction on access to this thesis.

22.Feb.91

(signature) (date)

ACKNOWLEDGMENTS

There are a number of people who have assisted with my research on this project. My supervisor, Professor Howard Choat provided much needed guidance and support throughout this project. His new-found interests in squids resulted in many interesting discussions and new ideas. His enthusiasm never waned (even through difficult times - such as the time I accidently embedded a squid jig in the skin of his back, during a research trip aboard the university vessel). My wife has provided unceasing help and support in many areas, throughout the years of this research. I would like to thank the crew of the 'James Kirby' who provided much needed assistance for the trawling trips. Many JCU students were also a great help during many of the vessel trips also. My associates in the Marine Biology lab (Frank Hoedt, Brett Molony and Lou) contributed to the interesting work environment of the lab. Many thanks to Frank who assisted with most of the trawling trips and a number of near-shore collecting trips. Natalie Moltschaniwskyj provided assistance with statistical analysis and provided some statoliths for examination. Leigh Winsor assisted with histological examination of the gonad material, Zolly Florian assisted with photography, Ann Sharp prepared the majority of tables and Bronwyn Scott provided specimen drawings. I would like to thank Dr. C.C. Lu who provided useful information. Dr. Lu and Mark Norman also assisted with research while I was in Melbourne. I would like to thank Roger Hanlon who sent statoliths and provided age information on cultured individuals of *Sepioteuthis lessoniana*. I would especially like to thank Dr. Ross Alford who assisted with theoretical aspects of curve-fitting and who offered editorial help on chapter seven. Last but not least I would like to thank my parents who have done all they could over the past years to encourage me in my studies.

ABSTRACT

Growth and ageing research was undertaken for squid and sepioid populations in waters off the Townsville region, North Queensland, Australia. The study species were the sepioid *Idiosepius pygmaeus,* and the loliginid squids *Loliolus noctiluca, Loligo chinensis, Loligo* sp. 1 and *Sepioteuthis lessoniana.* Age and growth parameters were determined by enumerating growth rings within the statolith microstructure of each of the species. Various mounting and grinding/polishing techniques were employed to reveal the growth rings. Daily periodicity in statolith growth rings was demonstrated to exist in 24 individuals in four of the study species; *I. pygmaeus* (6), *L. noctiluca* (9), *L. chinensis* (2) and *S. lessoniana* (7). Ring periodicity was determined by staining the statoliths *in situ* with tetracycline or calcein, and then maintaining the individuals in captivity to compare the rings laid down to the number of elapsed days. Double staining techniques were also employed to determine the rings laid down between stainings.

Field captured individuals of each of the study species were aged to construct growth curves. Growth was found to be rapid and maturity was found to be reached surprisingly fast. Tropical squid and sepioid growth is more correctly measured in days rather than months or years. The ageing studies with all five species did not reveal any individuals older than 200 days.

The ageing techniques developed were employed to discern any seasonality in squid and sepioid growth patterns. Regular sampling of *I. pygmaeus* and *L. chinensis* revealed different patterns of abundance, with *I. pygmaeus* more common during the winter period while *L. chinensis* was more abundant during the summer period.

Comparing growth based on statolith ageing to growth based on ELEFAN analysis on length frequency data revealed two diverging results. Length frequency analysis suggested that squid growth was asymptotic and that the life cycle was perennial. In contrast ageing research revealed that life span was short and that growth was rapid and non-asymptotic.

Seasonal size-at-age data for *I. pygmaeus* and *L. chinensis* revealed different patterns of growth during different seasonal periods. For *L. chinensis* growth was considerably slower during the winter period. For *I. pygmaeus* slower growth was also observed during the cooler period of the year. However, there was considerable scatter in the size-at-age data, probably as a result of greater variability in the near-shore environment. Differences were also detected in the relative statolith size in individuals of *L. chinensis* , with winter squids having larger statoliths for any given length than their summer counterparts. Alternatively, at comparable ages, winter squids had smaller statoliths than their summer counterparts, however, with increasing age, the longer-lived winter squids eventually obtained larger relative statoliths.

Determining individual size-at-age allowed for a more detailed understanding of age specific reproductive patterns. Male individuals of *Loligo chinensis* matured at a greater age in July (winter) than in January (summer) and no mature females were found in July. These age specific maturity patterns could not be discerned by an analysis of individual size. Development of the nidamental gland and hectocotylus was shown to follow a similar pattern to gonad development.

Mature individuals of *L. chinensis* were found throughout the year (except

July, 1989 for females). However, there was considerable fluctuations in the gonadosomatic index for both sexes with largest relative gonad sizes achieved during October for both years studied. This pattern appeared to be real and not biased by variation in the size of individuals captured during different months of the year.

Idiosepius pygmaeus showed a different pattern in gonad growth with cooler season (spring) sepioids growing older and having larger gonads than warmer season (autumn) individuals, despite the fact that there was very little difference in individual size between the two seasons. Measurement of oocyte diameters within the ovaries of two *I. pygmaeus* females suggested that this species was a serial spawner. Maintenance experiments of captive *I. pygmaeus* females confirmed that this species lays its eggs in repeated batches, rather than all at once. Maximum egg output recorded was 922 eggs produced in 15 days. Moreover, histological examination of the oocyte size distribution of all five study species suggested that they were serial spawners, since a variety of oocyte sizes were present within the ovary.

More relevant tropical squid growth models could be developed as a result of obtaining individual size-at-age data. All the five study species displayed allometric growth, with *Loligo chinensis* and *Loligo* sp. 1 displaying significant differences in the length-weight relationship between males and females, while *Idiosepius pygmaeus* revealed sex-related differences in slope elevation of the L-W relationship.

Detailed growth models were developed for *L. chinensis* and *S. lessoniana*. *Loligo chinensis* were shown to exhibit exponential growth with a considerable

proportion of the lifespan spent as juveniles. There was no significant difference between the growth curves of male and female *L. chinensis* in either growth in length or weight. The growth of *S. lessoniana* could not be modelled with a single equation. Therefore, an exponential curve was fitted to the size-at-age data (for both mantle length and weight) for the first 70 days, while growth from 70 to 153 days could be described by a linear equation. These growth models were compared to growth curves developed for other loliginids raised in captivity. *Loligo chinensis* was found to grow faster than other temperate loliginids, while the growth of *S. lessoniana* revealed a remarkable similarity to the form of growth of the tropical *S. sepioidea.* Length-at-age data for *Loligo opalescens* was found to not differ greatly from results of growth of this species in captivity, although field individuals appeared to grow somewhat faster than captive individuals.

Very clear growth rings were also observed within the statolith microstructure of the giant squid *Architeuthis*, which suggested that ageing research and growth modelling based on size-at-age data could be expanded to a variety of other species of oceanic squids. Statolith growth ring analysis is thus one means to obtain important growth parameters for squid species in which we have little biological information for.

TABLE OF CONTENTS

FRONTISPIECE ii

STATEMENT ON ACCESS TO THESIS iv

ACKNOWLEDGMENTS v

ABSTRACT vi

TABLE OF CONTENTS x

LIST OF TABLES xvii

LIST OF FIGURES xix

DECLARATION xxiii

CHAPTER ONE : GENERAL INTRODUCTION

CHAPTER TWO : SPECIES STUDIED, HABITATS AND GENERAL BIOLOGY

2.1 Species studied 8

2.1.1 *Idiosepius pygmaeus* 8

2.1.1.1 Habitat and biology of *I. pygmaeus* 9

2.1.2 *Sepioteuthis lessoniana* 11

2.1.3 *Loliolus noctiluca* 12

2.1.4 *Loligo chinensis* 13

2.1.5 *Loligo* sp. 1 14

CHAPTER THREE : GENERAL METHODS

3.1 Study area 16

3.2 The near-shore environment 17

3.3 Offshore sampling and jigging 17

3.4 Preservation of samples 18

3.5 Terminology 18

3.5.1 Larvae/paralarvae/juveniles/subadults 19

CHAPTER FOUR : STATOLITH ANALYSIS AND GROWTH RING VALIDATION

4.1 INTRODUCTION 24

4.2 MATERIALS AND METHODS 27

4.2.1 Statolith analysis 28

4.2.2 Maintenance and tetracycline staining 31

4.2.2.1 Collection of live individuals 31

4.2.2.2 Chemical staining of statoliths 31

4.2.2.3 Maintenance 32

4.3 RESULTS 33

4.3.1 *Idiosepius pygmaeus* 33

4.3.1.1 Statolith structure and microanatomy 33

4.3.1.2 Sexual dimorphism and growth 35

4.3.2 *Sepioteuthis lessoniana* 36

4.3.2.1 Tetracycline staining 36

4.3.2.2 Age and growth 37

4.3.3 *Loliolus noctiluca* 37

4.3.3.1 Tetracycline staining 38

4.3.3.2 Age and growth 39

4.3.4 *Loligo chinensis* 39

4.3.4.1 Tetracycline staining 40

4.3.4.2 Age and growth 40

4.3.5 *Loligo* sp. 1 40

4.3.5.1 Age and growth 41

4.3.6 Form of growth and comparison with other species 41

4.4 DISCUSSION 43

4.4.1 The statolith as a tool for squid growth studies 43

4.4.2 Growth in tropical Australian near-shore squids 47

CHAPTER FIVE : THE PATTERN OF AGE AND SEASONAL SPECIFIC EVENTS

5.1 INTRODUCTION 65

5.2 MATERIALS AND METHODS 67

5.2.1 Offshore sampling for loliginid squids 68

5.2.2 Statolith growth analysis of *L. chinensis* 69

5.2.3 Inshore population analysis of *I. pygmaeus* 70

5.2.4 *Acetes* analysis 71

5.2.5 Statolith age analysis of *I. pygmaeus* 72

5.2.6 Length frequency analysis 72

5.3 RESULTS 73

5.3.1 Loliginid abundance 73

5.3.2 Length frequency of *L. chinensis* 74

5.3.3 *I. pygmaeus* abundance 75

5.3.4 Length frequency of *I. pygmaeus* 76

5.3.5 Use of ELEFAN for length frequency analysis 77

5.3.6 Incorporation of ageing methods to determine seasonal influences on growth 79

5.3.6.1 *Loligo chinensis* 80

5.3.6.2 *Idiosepius pygmaeus* 82

5.3.7 Statolith length analysis 84

5.3.7.1 Statolith length versus mantle length 84

5.3.7.2 Statolith length versus age 84

5.4 DISCUSSION 84

5.4.1 Population variability over time 84

5.4.1.1 Offshore 84

5.4.1.2 Inshore 86

5.4.2 Length frequency analysis 88

5.4.3 Using ageing research to interpret seasonal changes in growth 90

5.4.3.1 Seasonal growth patterns of *L. chinensis* 90

5.4.3.2 Seasonal growth patterns of *I. pygmaeus* 92

5.4.4 Somatic versus statolith growth 93

CHAPTER SIX : REPRODUCTIVE BIOLOGY

6.1 INTRODUCTION 114

6.2 MATERIALS AND METHODS 116

6.2.1 Analysis of reproductive structures 116

6.2.2 Gonadosomatic and nidamental gland/mantle length indices 117

6.2.3 Ovary analysis 118
6.2.4 Egg production 118
6.2.5 Histological examination of ovaries 118
6.3 RESULTS 119
6.3.1 Growth of the gonad of *L. chinensis* with age 119
6.3.1.1 Males 119
6.3.1.2 Females 120
6.3.2 Gonad soma relationships of *L. chinensis* 121
6.3.3 Reproductive indices of *L. chinensis* 122
6.3.4 Growth of the gonad of *I. pygmaeus* with age 124
6.3.4.1 Males 125
6.3.4.2 Females 125
6.3.5 Gonad soma relationships of *I. pygmaeus* 126
6.3.6 Secondary sexual characteristics of *L. chinensis* 126
6.3.7 Ovary analysis/egg production 127
6.4 DISCUSSION 128
6.4.1 *Loligo chinensis* 130
6.4.1.1 Seasonality of reproductive investment 132
6.4.2 *Idiosepius pygmaeus* 134
6.4.3 Secondary sexual characteristics of *L. chinensis* 136
6.4.3.1 Nidamental gland length 136
6.4.3.2 Hectocotylus length 137
6.4.4 Tropical squid and sepioid reproductive patterns 138
6.4.5 Semelparity or iteroparity? 140

CHAPTER SEVEN : ALLOMETRY AND GROWTH MODELLING

7.1 INTRODUCTION 156

7.2 MATERIALS AND METHODS 158

7.2.1 Allometry 160

7.2.2 Growth modelling 158

7.2.3 *Loligo opalescens* age analysis 160

7.2.4 *Architeuthis* age analysis 160

7.2.5 Digitising of published growth data 161

7.3 RESULTS 161

7.3.1 Allometry 161

7.3.2 Growth modelling 163

7.3.2.1 *Loligo chinensis* 163

7.3.2.2 *Sepioteuthis lessoniana* 164

7.3.3 Comparisons of growth models with other research 166

7.3.3.1 *Loligo chinensis, Loligo forbesi* and *Loligo opalescens* . . . 166

7.3.3.2 *Sepioteuthis lessoniana* and *Sepioteuthis sepioidea* 167

7.3.3 Cuttlefish 168

7.3.4 Growth of the giant squid *Architeuthis* 168

7.4 DISCUSSION 169

7.4.1 Allometry 169

7.4.2 Modelling of squid growth 172

7.4.3 Growth models derived from culture experiments 173

7.4.4 Growth models derived from statolith ageing 175

7.4.5 Analysis of Natsukari's method 176

7.4.6 Growth of *L. chinensis* and *S. lessoniana* 177

7.4.7 Future considerations 178

CHAPTER EIGHT : GENERAL DISCUSSION AND CONCLUSIONS

8.1 Why can't squid growth be modelled by teleost models? . . 201

8.1.1 The reliability of cephalopod length frequency data 204

8.2 Age data and reproductive events 205

8.3 Coleoid growth versus nautiloid growth 206

8.4 The paradox of the extended juvenile growth phase 206

THESIS REFERENCES 208

APPENDICES 221

LIST OF TABLES

CHAPTER FOUR

4.1 Age validation information for *Idiosepius pygmaeus*.

4.2 Age validation information for *Sepioteuthis lessoniana*.

4.3 Tetracycline staining and statolith ring counts for *Loliolus noctiluca*.

4.4 Tetracycline injection and statolith ring counts for *Loligo chinensis*.

4.5 Summary of species and number of individuals used in chemical staining of statoliths.

4.6 Maximum sizes attained for the study species from the sampling program, and as recorded from the literature.

CHAPTER FIVE

5.1 Comparison of the number of rings extrapolated from submarginal areas of the statolith compared with the actual rings counted at the marginal areas of equivalent radius in specimens with clear statoliths.

5.2 *Acetes* abundance estimates applied to each dip-net sample used in obtaining a Relative *Acetes* Abundance Index.

5.3 Recent published information on squid lifespans.

5.4 Regression equations for the length-at-age data for *Loligo chinensis* sampled during January (summer) and June (winter), by sex.

5.5 *Loligo chinensis*. Mean growth rates expressed as mm day^{-1} for summer and winter samples of male and female *L. chinensis*.

5.6 *Loligo chinensis*. Summary of the comparisons of regression equations.

5.7 *Loligo chinensis*. Mean length and age $\pm$ standard error of squids between 90 and 110 mm mantle length for males and females collected at two times within each season.

5.8 *Idiosepius pygmaeus*. Regression equations for the length-at-age data sampled from different seasonal periods, by sex.

5.9 *Idiosepius pygmaeus*. Mean growth rates expressed as mm day^{-1} for each combination of sex and sampling period.

CHAPTER SEVEN

7.1 Summary of the comparisons of logged length-weight regression equations for each of the study species.

7.2 Values of the constants *a* and *b* from the log-transformed length-weight regression analysis.

7.3 Summary of the comparisons of regression equations for male and female *Loligo chinensis* for age versus log-weight and age versus log-length.

LIST OF FIGURES

CHAPTER TWO

2.1 Relative sizes of four of the study species.

CHAPTER THREE

3.1 Squid and sepioid collecting sites in the Townsville region.

3.2 Photograph of the Townsville Harbour and surrounding region.

3.3 Important collecting localities in the Townsville Harbour region.

CHAPTER FOUR

4.1 Light micrographs of *Idiosepius pygmaeus* statoliths.

4.2 Relationship between age (statolith ring number) and mantle length for field captured male and female *Idiosepius pygmaeus*.

4.3 Light micrographs of *Sepioteuthis lessoniana* statoliths.

4.4 Relationship between age (statolith ring number) and mantle length for field captured male, female and juvenile *Sepioteuthis lessoniana* specimens.

4.5 Daily growth rings within the statoliths of *Loliolus noctiluca* and *Loligo chinensis*.

4.6 Relationship between age (statolith ring number) and mantle length for field captured male, female and juvenile *Loliolus noctiluca* specimens.

4.7 Relationship between age (statolith ring number) and mantle length for male, female and juvenile field captured *Loligo chinensis* specimens.

4.8 Relationship between age (statolith ring number) and mantle length for field captured male and female *Loligo* sp. 1.

4.9 Length-at-age data for male, female and juvenile *Sepioteuthis lessoniana* from this study shown with length-at-age data for cultured *S. lessoniana* specimens of known age.

CHAPTER FIVE

5.1 Total percentage catch of loliginid squids (*Loligo chinensis* and *Loligo* sp. 1) captured in trawl samples during each sampling trip.

5.2 Mean number of individuals of *Loligo chinensis* and *Loligo* sp. 1 captured per trawl for each sampling trip.

5.3 Percentage length frequency distributions for all individuals of *Loligo chinensis* captured during each sampling trip.

5.4 Numbers of individuals of *Idiosepius pygmaeus* counted along the western breakwater.

5.5 Numbers of individuals of *Idiosepius pygmaeus* collected along the eastern breakwater, superimposed over the numbers of *I. pygmaeus* counted along the western breakwater.

5.6 The Relative *Acetes* Abundance Index calculated for one sampling trip each month, superimposed over the numbers of individuals of *Idiosepius pygmaeus* collected along the easern breakwater.

5.7 Length frequency distribution for male and female individuals of *Idiosepius pygmaeus* captured along the eastern breakwater.

5.8 Growth curves constructed for ELEFAN analysis of squid length frequency.

5.9 Relationships between mantle length and age, and weight and age for two samples of individuals of *Loligo chinensis* collected during summer (January) and winter (July).

5.10 Least squares regression lines for the relationship between mantle length and age for both summer (January) and winter (July) samples of *Loligo chinensis*.

5.11 The relationship between mantle length and age for individuals of *Idiosepius pygmaeus* collected from four time periods.

5.12 The relationship between statolith length and mantle length, and statolith length and age for summer (January) and winter (July) samples of *Loligo chinensis*.

5.13 Fitted curves and regressions for statolith length and mantle length, and statolith length and age for *Loligo chinensis*

CHAPTER SIX

6.1 The relationship between gonad weight and age for male and female individuals of *Loligo chinensis* collected in summer (January) and winter (July).

6.2 The relationship between gonad weight and mantle length for male and female individuals of *Loligo chinensis* collected in summer (January) and winter (July).

6.3 Mean monthly gonadosomatic index for individuals of *Loligo chinensis* collected over the study period.

6.4 Comparison of nidamental gland/mantle length index with gonadosomatic index for female *Loligo chinensis* collected over the study period.

6.5 Mean mantle length for individuals of *Loligo chinensis* used in gonad weight analysis.

6.6 The relationship between gonad weight and age for male and female individuals of *Idiosepius pygmaeus* collected in autumn and spring.

6.7 The relationship between gonad weight and mantle length for male and female individuals of *Idiosepius pygmaeus* collected in autumn and spring.

6.8 The relationship between nidamental gland length and age; and nidamental gland length and mantle length for female individuals of *Loligo chinensis* collected during summer (January) and winter (July).

6.9 The relationship between hectocotylus length and age; and hectocotylus length and mantle length for male individuals of *Loligo chinensis* collected during summer (January) and winter (July).

6.10 Oocyte diameter within the ovary of two female individuals of *Idiosepius pygmaeus*.

6.11 Cumulative egg output for female individuals of *Idiosepius pygmaeus* maintained in captivity.

6.12 Histological sections of ovaries of the five study species, showing a range in oocyte size.

CHAPTER SEVEN

7.1 Arithmetic and logarithmic length-weight relationships for *Idiosepius pygmaeus*.

7.2 Arithmetic and logarithmic length-weight relationships for *Loliolus noctiluca*.

7.3 Arithmetic and logarithmic length-weight relationships for *Loligo chinensis*.

7.4 Arithmetic and logarithmic length-weight relationships for *Loligo* sp. 1.

7.5 Arithmetic and logarithmic length-weight relationships for *Sepioteuthis lessoniana*.

7.6 Length-weight relationships for *Sepioteuthis lessoniana* from Australian, Indian, Japanese field and Japanese cultured populations.

7.7 Relationships between mantle length and age, and weight and age, for individuals of *Loligo chinensis* and *Loligo* paralarvae.

7.8 Exponential growth curves determined for *Loligo chinensis*, for both growth in mantle length and weight.

7.9 Relationships between mantle length and age, and weight and age, for *Sepioteuthis lessoniana* from hatchling to adult.

7.10 Relationships between mantle length and age, and weight and age, for *Sepioteuthis lessoniana* displayed on a semi-log plot.

7.11 Exponential/linear growth curves developed for *Sepioteuthis lessoniana* for both growth in mantle length and growth in weight.

7.12 Growth curve developed for *Loligo chinensis* compared to growth curves determined for *Loligo opalescens* and *Loligo forbesi*.

7.13 Length-at-age data for *Loligo opalescens* captured in the vicinity of Monterey Bay, California, displayed with size-at-age data for this species determined from culture experiments.

7.14 Growth curve developed for males and juveniles of *Sepioteuthis lessoniana* from this study, shown with growth curve developed for *Sepioteuthis sepioidea* based on culture experiments.

7.15 Growth curves developed for three species of cuttlefish.

7.16 Growth rings within the statolith microstructure of the juvenile *Architeuthis* specimen from this study.

7.17 Length-at-age data for *Photololigo edulis* (data for warm-season brood, from Natsukari *et al.*, 1988) with fitted exponential growth curve.

DECLARATION

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

G. D. Jackson
22 February 1991