

AUSTRALIAN MUSEUM SCIENTIFIC PUBLICATIONS

Harriott, V., 1982. Papers from the Echinoderm Conference. 4. Sexual and asexual reproduction of *Holothuria atra* Jaeger at Heron Island Reef, Great Barrier Reef. *Australian Museum Memoir* 16: 53–66, ISBN 0-7305-5743-6. [31 December 1982].

doi:10.3853/j.0067-1967.16.1982.358

ISSN 0067-1967

Published by the Australian Museum, Sydney

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THE AUSTRALIAN MUSEUM, SYDNEY

MEMOIR 16

Papers from the
Echinoderm Conference

THE AUSTRALIAN MUSEUM
SYDNEY, 1978

Edited by

FRANCIS W. E. ROWE

The Australian Museum, Sydney

Published by order of the Trustees
of The Australian Museum

Sydney, New South Wales, Australia
1982

Manuscripts accepted for publication 27 March 1980

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FOREWORD

Since the first major Symposium on Echinoderm Biology was held in London in 1966, sponsored by the Royal Zoological Society, at least six subsequent meetings have been organised by echinodermologists. These have been held in Washington D.C., U.S.A. (2), Rovinj, Yugoslavia (1), Sydney, Australia (1), London (1); the last two meetings (Sydney and London), within the same year (1978), and Brussels, Belgium. Also, at least four meetings are known to have been held in U.S.S.R. Such has been the surge of interest in the study of echinoderms over the past decade, that there is now a demand for the organisation of regular, and more frequent, meetings. The international representation at these meetings indicates the enormous involvement and co-operation which now exists between colleagues working in this exciting field, the world over.

It is more than evident that the satisfaction and pleasure expressed by Professor Norman Millott, in his foreword to the first Symposium volume (1967), at the resurgence of interest in Echinoderm Biology has been clearly justified and can continue so to be.

This volume presents twelve of the forty-one contributions offered at the Echinoderm Conference, Sydney, 1978. The papers are representative of the wide coverage of topics dealt with during the Conference, including echinoderm palaeontology, physiology, reproduction, ecology, behaviour and taxonomy.

To the speakers and chairmen, and to all those who attended the Sydney Conference, I convey my thanks. I must also thank my Technical Officer, Ms Jan Marshall, and Dr Susan Oldfield (Queen's Fellow at The Australian Museum, February, 1977-1979) for their unstinting assistance in the organisation of the Conference. Thanks are also due to the Department of State Fisheries (N.S.W.), Taronga Park Zoo, McWilliams Wines Pty, Leo Buring Wines Pty, Qantas Airways Ltd, and Trans-Australia Airlines (T.A.A.). To The Australian Museum Society (TAMS) I extend a special thanks for assistance.

This Conference could not have been held without the tremendous support and encouragement afforded to the organiser by Dr D. J. G. Griffin, Director, The Australian Museum, and the very generous financial support of the Trustees of the Museum, to both of whom I offer my very sincere thanks.

DECEMBER 1979

FRANCIS W. E. ROWE

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4. SEXUAL AND ASEXUAL REPRODUCTION OF *HOLOTHURIA ATRA* JAEGER AT HERON ISLAND REEF, GREAT BARRIER REEF

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SUMMARY

H. atra is the most common epifaunal holothurian on the reef flat at Heron Island. The gonad maturation cycle of *H. atra* was followed using gonad index estimations and histological examination. Gonad samples were taken at intervals of 6 to 8 weeks for 18 months. Mature gonads occurred in most samples, and gonad maturity peaked twice; in early winter and in summer. Sex ratio of female to male animals was not significantly different from a 1:2 ratio. Sex ratio ranged from 1:8.5 in animals weighing less than 100 g, to 1:0.7 in those over 1,000 g. *H. atra* commonly reproduces asexually by transverse binary fission. In 21 samples, each of approximately 50 animals, 6% to 70% of individuals were detectable products of asexual reproduction. Occurrence of frequent asexual reproduction compounds difficulties in estimation of growth parameters from data such as size-frequency distributions and growth increments.

INTRODUCTION

Holothurians are amongst the most common coral reef macro-invertebrates, but little information is available on their reproductive biology (Bakus, 1973). An understanding of reef systems requires data on the population dynamics and patterns of recruitment of these, and many other reef species.

Temperate holothurians, in common with other temperate marine invertebrates, generally spawn for a limited period during spring or summer (Booolootian, 1966). Tropical species, however, exhibit a variety of spawning patterns. Holothurians are also known to reproduce asexually, by transverse binary fission (Hyman, 1955; Bonham and Held, 1963).

Holothuria atra Jaeger is widely distributed in the Indo-West Pacific region, and is the most common epifaunal holothurian on the reef flat at Heron Island. In this habitat, it is generally found on sandy substrata.

Pearse (1968) studied sexual reproduction of *H. atra* at several low latitude sites in the tropical Indo-Pacific. Because individuals with mature gonads were found throughout the year, he concluded that spawning was asynchronous. He predicted that populations distant from the equator would have more restricted spawning periods.

Bonham and Held (1963) reported asexual reproduction by fission in *H. atra* at Rongelap Atoll, Marshall Islands, and suggested that fission occurred commonly. Ebert (1978) interpreted the apparently high rate of asexual reproduction in *H. atra* at Enewetak Atoll, as an adaptation enabling the species to span periods of unsuccessful recruitment from the sexual phase.

The relative frequency of recruitment from sexual and asexual modes of reproduction is a potentially important life history parameter. This paper reports on sexual and asexual reproduction in *H. atra* at different sites on Heron Island reef, in the Capricorn Group, at the southern extremity of the Great Barrier Reef (Lat. 23° 27' S).

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Australian Museum Memoir No. 16, 1982, 53-66.

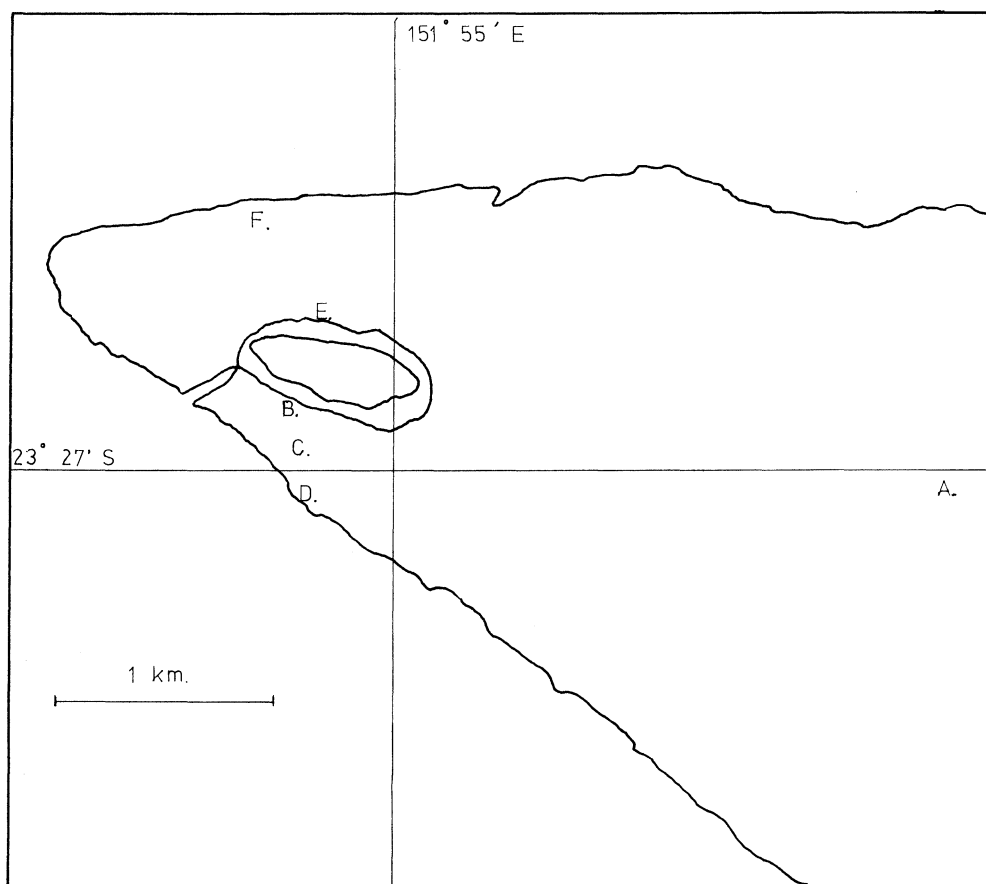


Fig. 1. Heron Island reef showing sample sites. A = shallow lagoon; B = S. W. reef flat, gutter; C = S. W. reef flat, mid-reef; D = S. W. reef flat, crest; E = N. E. reef flat, inshore; F = N. E. reef flat, rubble crest.

METHODS

Sites sampled on Heron Reef during the course of the study are shown in Figure 1.

1. SEXUAL REPRODUCTION

The reproduction cycle of *H. atra* was studied over 18 months, from December, 1976 to June, 1978. Gonads were sampled at intervals of 6 to 8 weeks during this period. Sexual reproduction was studied in 2 ways; (a) by use of gonad index estimation, and (b) by histological examination of excised gonads.

(a) Gonad index estimation. For each sample, individuals of *H. atra* were collected from the lagoon of Heron Island reef (fig. 1; site A). Sample size ranged from 12 to 24, with a mean sample size of 16 individuals. The animals were taken to the laboratory and maintained overnight in aerated aquaria to allow emptying of the guts. Wet weight of the animals was measured to the nearest 5 g, and gonads were excised and weighed to the nearest 0.01 g. The gonad index was calculated as the ratio of wet gonad weight to wet body weight, expressed as a percentage, for each individual. The mean gonad index (\pm S.E.) was calculated for each of the 13 samples obtained.

(b) Histology of gonads. Excised gonads were preserved and fixed in alcoholic Bouin's fixative and stored in 70% ethyl alcohol. They were dehydrated, cleared, embedded in paraffin wax, and sectioned at a nominal thickness of 10 μ m. Sections were stained with haematoxylin and eosin.

Gonads were assigned to one of three classes of maturation, derived from those recognised by Tanaka (1958) —

- (i) Resting stage and indeterminate gonads.
- (ii) Recovery stage and growing stage gonads.
- (iii) Mature stage and shedding stage gonads.

The sex ratio was recorded for individuals of a wide range of weights. These animals were collected from several habitats.

2. ASEQUAL REPRODUCTION

Samples of 33 to 100 individuals, each weighing less than 90 g, were collected from 6 habitats, A to F (fig. 1). Habitats A, B and C were sampled five times (between August, 1977 and June, 1978), habitat D was sampled four times, and habitats E and F were sampled once only. Each individual was dissected and examined for the following signs of recent binary fission, as recognised by Crozier (1917).

- a. An abnormally large or small calcareous ring.
- b. A change in colour or texture of the internal body wall at the region of regeneration.
- c. The absence or smallness of either anterior or posterior body organs.
- d. A narrowing of the five longitudinal muscle bands at the line of division.

For each fissioned individual, the degree of regeneration following fission was determined, and scored on a scale of 0-3 by the following criteria —

0. No visible regeneration; very recent division.
1. First signs of regeneration of gut, mouth or anus; very small calcareous ring present (less than 5 mm diameter); body wall regrowth less than 1 cm in length.
2. Body organs regenerated but small; body wall regrowth 1-3 cm.
3. Complete regeneration of body organs; discernable as fission product by narrowing of muscle bands and difference in colour of body wall; body wall regrowth over 3 cm.

The percentages of fissioned individuals in early stages of regeneration (stages 0 and 1) were plotted against time to indicate changes in the frequency of recent division.

3. POPULATION SIZE STRUCTURE

Size-frequency distributions were used to ascertain population size structure in the habitats from which specimens had been examined for asexual reproduction. Samples of 80-300 individuals were weighed in the field to ± 5 g, and weights plotted to produce size-frequency histograms.

RESULTS

1. SEXUAL REPRODUCTION

From Figure 2, the plot of gonad index over time, seasonal variations in gonad index are apparent. Gonad index peaked at 1.8%, 2.7% and 1.2% in May, 1977, December, 1977 and May, 1978 respectively. Each peak was followed by a decrease in gonad index to 0.3% and 0.8% and 0.4% respectively, indicating possible spawnings during the months of May/June and December/January.

Seasonal changes in histological state of the gonads are recorded in Figure 3. Changes in percentages of mature gonads closely parallel changes in gonad index, indicating that, for this species, gonad index is a good measure of gonad maturity. The percentage of mature gonads peaked at 75% and 100% in May and December, 1977 respectively.

Histological data confirm that spawning follows these peaks in gonad maturity. A decrease in the percentage of mature gonads is accompanied by an increase in the percentage of histologically determined spawned gonads.

Spawning occurred later in summer 1977-78 than it did the previous year, when individuals had spawned by mid-December.

Differences in reproductive cycle between male and female individuals were indeterminable because of the small numbers of females in some samples (Table 1).

Hermaphroditic gonads, that is, those containing both male and female gonad elements, were detected in 2 of the 155 individuals examined.

Sex-ratio for individuals of *H. atra* from different samples is shown in Table 1. The sex ratios were tested for homogeneity using a X^2 test, and were found to be sufficiently homogeneous to permit pooling ($p > 0.05$). Pooled data were tested, and the ratio was found to differ significantly from 1:1 ($X^2 = 24.25$, $p < 0.01$), but was not significantly different from a 1:2 ratio of females to males ($X^2 = 0.04$, $p > 0.5$).

Figure 4 shows the relationship between sex and size (weight), for all individuals examined. Because of small sample size, results have been pooled for the large size classes. The relationship between sex and weight was tested using X^2 contingency table analysis, and sex was found to be dependent on size class ($p < 0.02$). In individuals weighing less than 100 g for which gonads are recorded, the ratio of females to males was 1:8.5 ($n = 21$); while in those individuals over 1,000 g, the ratio was 1:0.7 ($n = 11$).

2. ASEXUAL REPRODUCTION

Table 2 shows the percentages of detectable products of asexual reproduction in each sample, from the habitats indicated. Small individuals, i.e. those less than 100 g were sampled because fission products will eventually regenerate and become unrecognisable. Fission

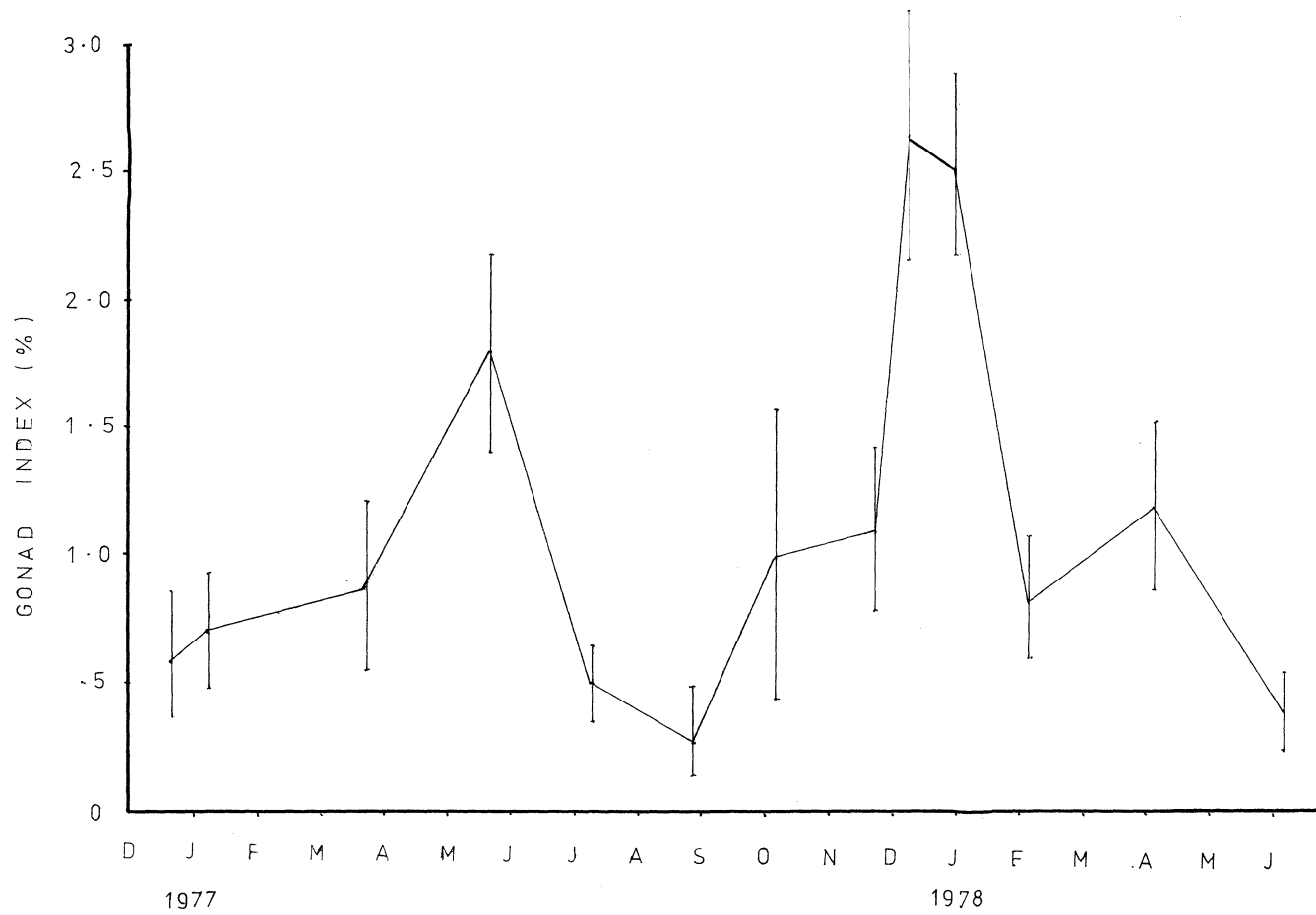


Fig. 2. Seasonal changes in mean gonad index of *H. atra* (December 1976-June 1978). Vertical lines show range of standard error.

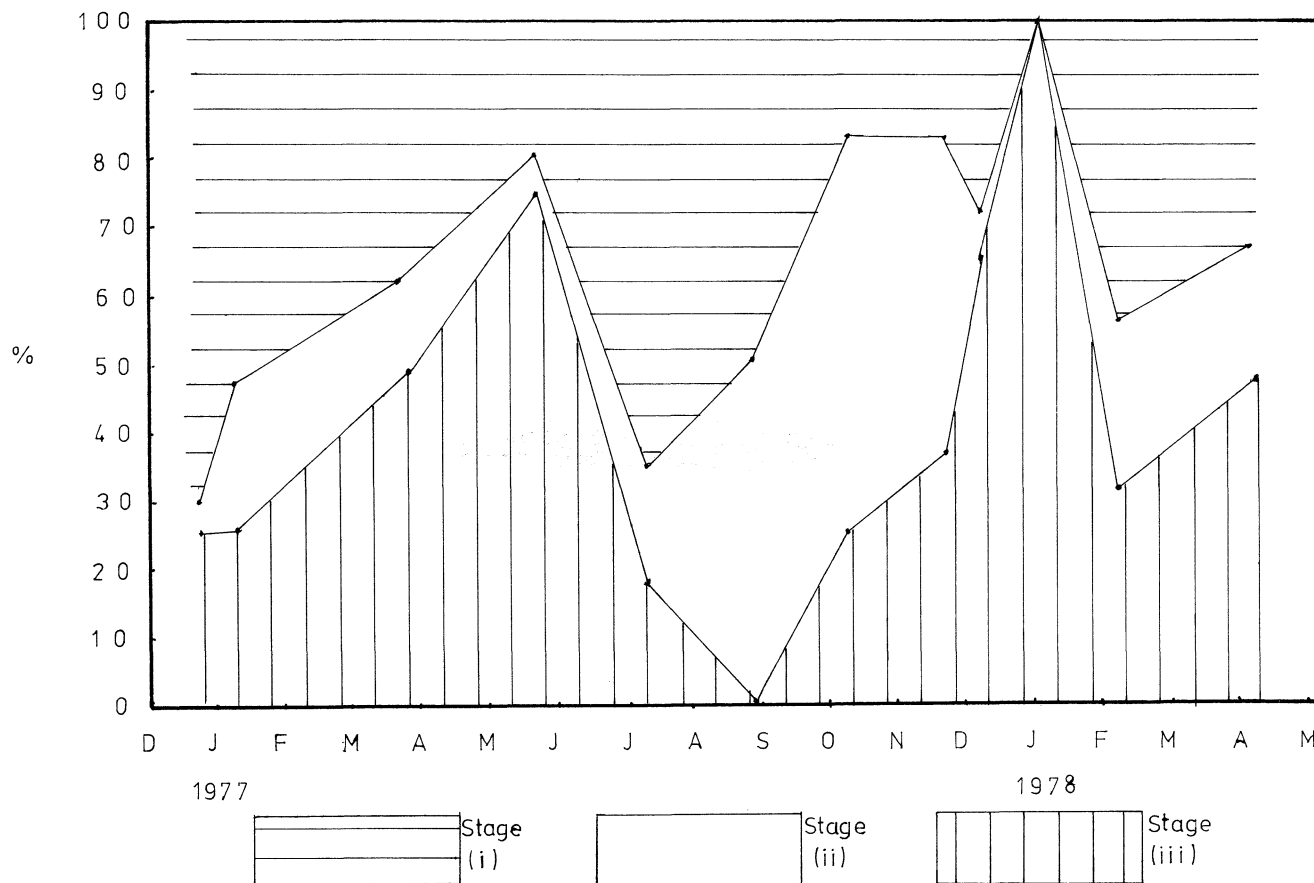


Fig. 3. Seasonal changes in gonad maturation of *H. atra* (December 1976 - April 1978), showing the percentages of individuals of each sample which were in the stages (i) Resting stage and indeterminate, (ii) Recovery and growing stage, (iii) Mature and shedding stage.

TABLE 1. Abundance of male and female *H. atra*, sampled from lagoon, unless specified.

	♀	♂
December 1976	6	3
January 1977	4	10
March, 1977	2	9
May, 1977	6	10
July, 1977	3	6
August, 1977	4	7
October, 1977	0	8
October, 1977 — Crest	6	4
November, 1977	5	16
November, 1977 — Flat	4	6
November, 1977 — Gutter	5	14
December, 1977	5	8
January, 1978	4	12
January, 1978 — Crest	4	4
February, 1978	5	10
April, 1978	4	9
n = 202	66	136

products were rarely detected in the individuals greater than 100 g that were sampled for gonads.

Differences in frequency of fission among these samples were tested using X^2 contingency table analysis, at the 95% confidence level. Several patterns are apparent from the data, e.g.:

- The frequency of asexual reproduction is significantly dependent on habitat for all months, with $p(X^2) < 0.001$, except in February 1978 when $p(X^2) = 0.006$.
- In the lagoon and reef crest, the percentage of fission products is dependent on time $p(X^2) > 0.005$.

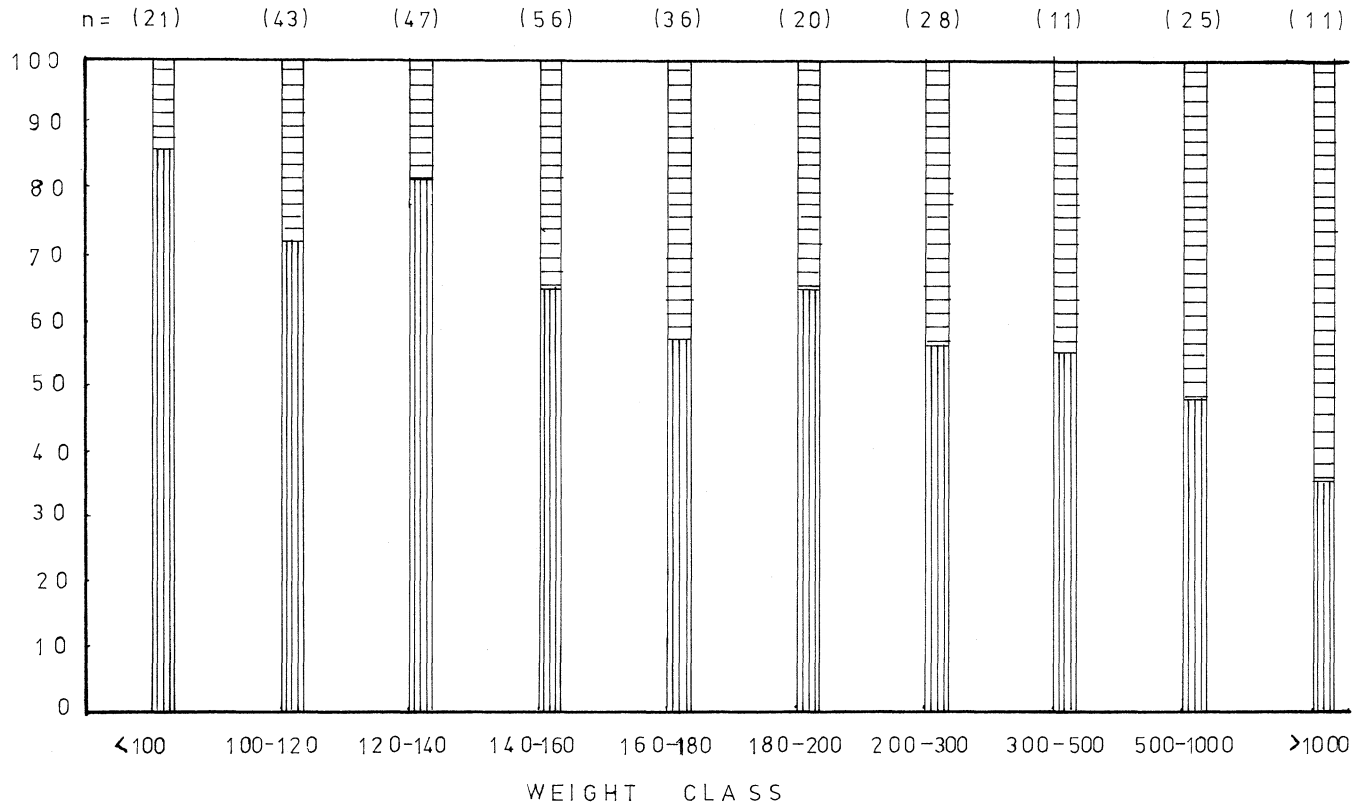
Figure 5 shows changes in the percentage of recent divisions (stage 0 and 1), over the period sampled, in the gutter habitat (fig. 1, site B). Division is more frequent in the period preceding August 1977 than in the period preceding June 1978. This result is supported by the changes in fission frequency with time in some habitats, and suggests that fission frequency is not constant throughout the year, but is maximal during limited periods.

The ratio of former posterior to former anterior ends was approximately 1:1, indicating a similar mortality rate for each section.

Fission rate appears to be approximately equal in males and females, although only a small percentage of fissioned individuals examined contained detectable gonads. Of the 38 individuals with visible gonads, 12 were female, 15 were male, and 11 were indeterminate. Although no detailed histological examination was made, gonads examined appeared to include all stages of gonad maturity.

3. POPULATION SIZE STRUCTURE

The size-frequency distributions obtained were variable over time and habitat, but frequently conformed with one of two general patterns, unimodal or bimodal (fig. 6). No consistent age-class groups were detectable. Samples from the inshore gutter area always had a



VICKI HARRIOTT

Fig. 4. Graph of changes in sex ratio with increasing weight. The ordinate represents the percentage of each weight class that was male (vertical stripes), and female (horizontal stripes).

TABLE 2. Percentages of *H. atra* samples (sample numbers in brackets) that were discernable products of asexual reproduction in 6 habitats of Heron Island reef from August 1977 to June 1978.

HABITAT	August 1977	October 1977	Nov./Dec. 1977	February 1978	April 1978	June 1978
S. W. Reef Flat						
Gutter	61% (51)		58% (56)	58% (52)	56% (50)	51% (50)
Crest	11% (44)		22% (58)	37% (48)	22% (50)	6% (50)
Mid-Reef	40% (33)			62% (51)	60% (45)	70% (46)
Lagoon		20% (65)	14% (50)	34% (50)	52% (50)	52% (52)
N.W. Reef Flat						
Rubble crest		47% (108)				
Inshore			50% (50)			

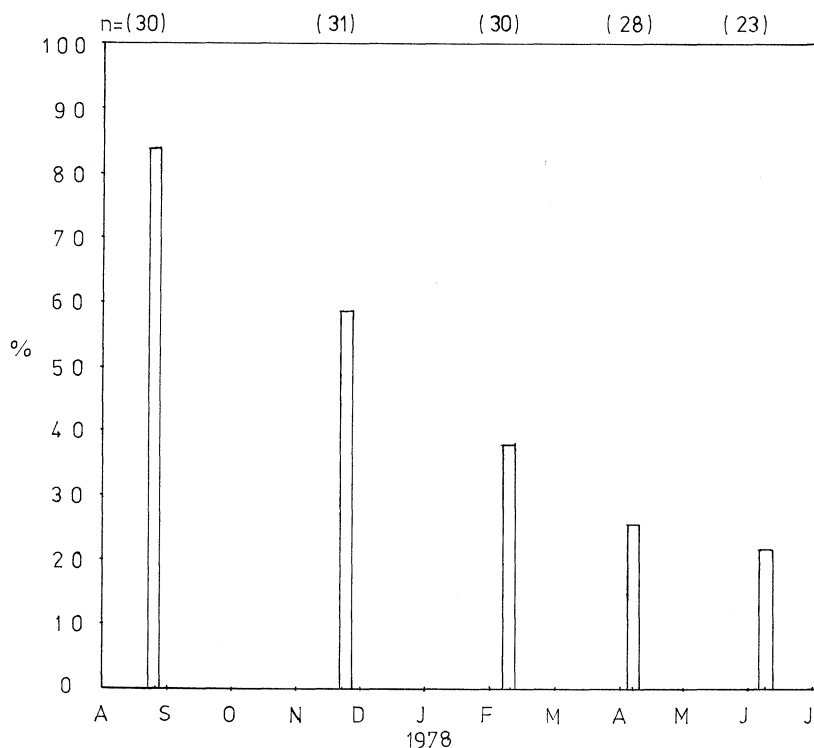


Fig. 5. Graph of percentage of fissioned individuals that were in early stages of regeneration i.e. stages 0 and 1, sampled from the S. W. reef flat gutter, from August 1977 to June 1978.

bimodal distribution, those from the reef-crest had a unimodal distribution, and samples from the lagoon and mid-reef had distributions that varied with time.

DISCUSSION

H. atra has a semi-annual reproductive cycle at Heron Island reef, and a large proportion of the population breeds in both winter and summer.

Until 1966, there was no record of semi-annual reproductive cycles in holothurians (Booolootian, 1966). Since then 2 species have been reported with this breeding pattern. *H. scabra* Jaeger in India spawns predominantly semi-annually, in summer and autumn (Krishnaswamy and Krishnan, 1967). The authors suggest that salinity changes, caused by fresh water influxes following monsoons, may induce spawning in *H. scabra* and other tropical marine animals. There are no comparable semi-annual salinity changes at Heron Island reef.

More recently, a temperate hermaphroditic species, *Leptosynapta tenuis* (Ayres), has been reported to have a semi-annual reproductive cycle (Green, 1978). The population spawned in the spring and in the fall, with a mid-summer cessation of reproductive activity. Green suggested that external factors, possibly temperature, might regulate the reproductive cycle.

A semi-annual reproductive cycle is well-known amongst other tropical marine invertebrates. The Great Barrier Reef Expedition reported a semi-annual spawning cycle (spring and autumn) in the echinoid *Tripneustes gratilla* (Linnaeus) (Stephenson, 1934). Both *T. gratilla* and *T. ventricosus* (Lamarck) vary in reproductive cycle with geographic location, but exhibit a tendency for semi-annual reproduction, and in some locations spawn in winter and summer (Pearse, 1974).

In his study of reproduction in tropical *H. atra*, Pearse (1968) found that spawning was asynchronous, mature gonads being present throughout the year. He suggested that breeding season would become more restricted with distance from the equator. This proposition is supported by the present study, since mature gonads were found in almost every sample, but the majority of individuals spawned in two limited periods.

The semi-annual reproductive cycle of *H. atra* is not typical of other species of holothurians studied at Heron Island reef. *H. impatiens* (Forsk.) (unpub. data) and *H. leucospilota* (Brandt) (S. Franklin, pers. comm.) are both synchronized annual breeders, spawning in spring or summer. Spawning in *H. edulis* (Lesson) is apparently non-synchronized and non-cyclic (unpub. data).

Several hypotheses may be proposed to account for the change in sex ratio of *H. atra* with increased size. Three hypotheses are presented here.

- a. Mortality rates of male and female animals may change throughout their life-span. Mortality rate may be high in female individuals before sexual maturity, and in male individuals after sexual maturity. It is difficult to postulate biotic or abiotic factors that might contribute to this differential mortality.
- b. A relatively higher rate of fission in male individuals than in females would lead to a higher incidence of males than females among small animals and a higher incidence of females than males among large animals. However, available data on sex of fission products (15 male, 12 female, 11 indeterminate) suggest that the sex ratio of fission products is approximately 1:1. Because of the small number of fission products for which sex data are available, this theory cannot be entirely discounted.
- c. Some proportion of the population of *H. atra* may exhibit protandrous

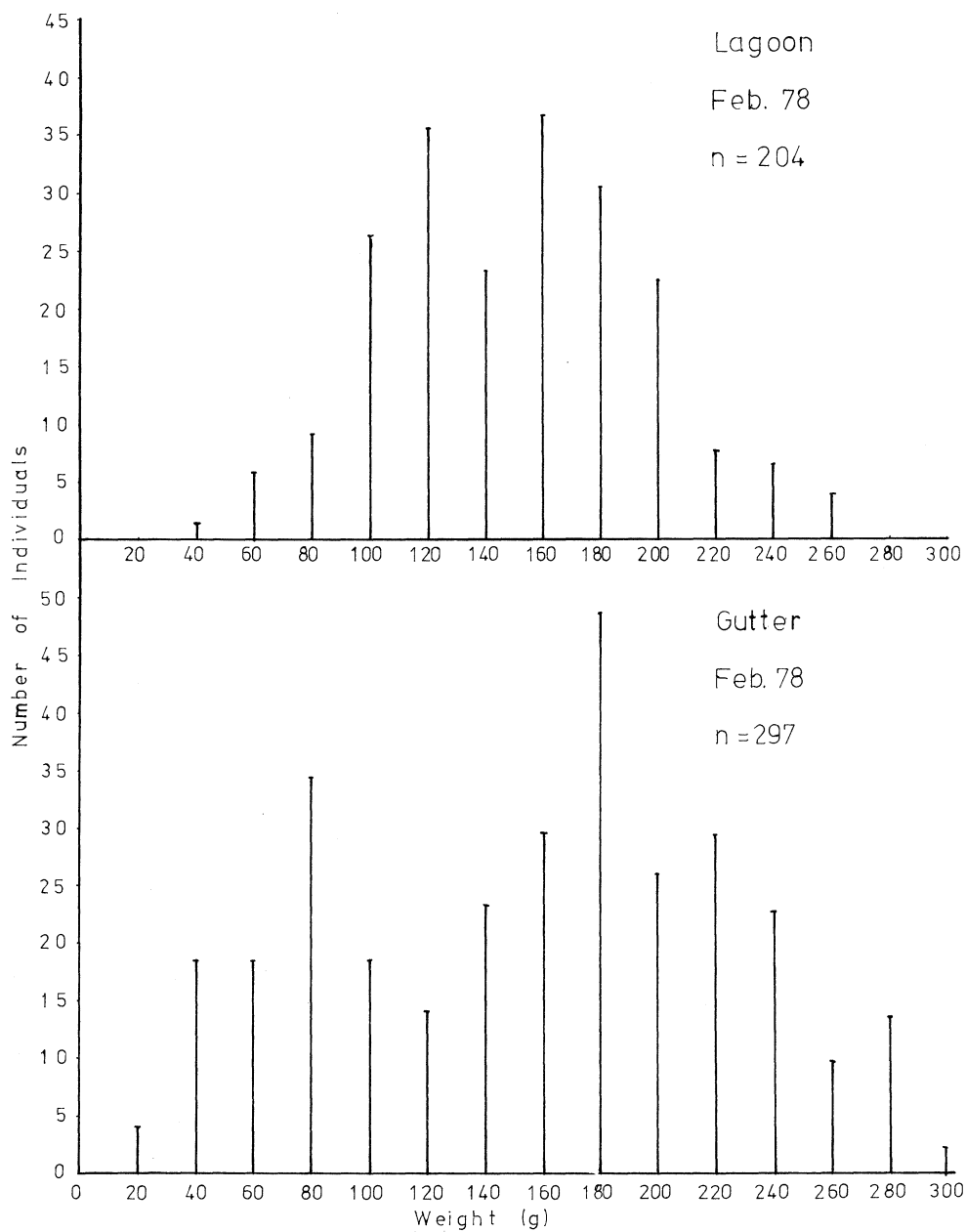


Fig. 6. Typical size-frequency distribution patterns of *H. atra*; unimodal (lagoon) and bimodal (gutter).

hermaphroditism. Hermaphroditism is common in holothurians and other echinoderms (Hyman, 1955), and protandrous hermaphroditism has been recorded for several echinoderms (Bacci, 1965). At some stage during their growth, a certain proportion of individuals may change from males to females. This hypothesis is difficult to test as gonads regress after each spawning, and may disappear before the development of new gonads. It is impossible to determine the sex of previous gonads. Two hermaphroditic gonads have been detected amongst those sectioned to determine the reproductive cycle. It is possible that individuals may change sex more than once during their lifetime.

Although transverse fission in holothurians is a commonly recorded phenomenon (Hyman, 1955; Bonham and Held, 1963), few studies include any quantitative data on the importance of asexual reproduction in the life-histories of the species. Crozier (1917) found evidence of binary fission in 11% of individuals of *H. surinamensis* Ludwig examined, and concluded that fission represented a regular means of multiplication in the species. Deichmann (1922) found 50% regenerating specimens of *H. difficilis* Semper, and 65% of *H. parvula* (Selenka), in samples studied. The mode of division in these species is apparently identical with that of *H. atra*. Fissioned and fissioning specimens of *Stichopus horrens* Selenka, *S. chloronotus* Brandt and *H. edulis* have been found by the author at Heron Reef, the latter commonly.

The frequency of asexual reproduction is related to habitat. In general at any one time, fission frequency is greater in the gutter and mid-reef habitats than in the S.W. reef-crest and lagoon habitats. From the present study, it is impossible to distinguish causative factors in the relationships between habitat and frequency of asexual reproduction. Pearse (1968) suggested that fission may be more frequent in *H. atra* in surf-swept intertidal areas. This is supported by the low fission frequency of the lagoon, but contradicted by the unusually low rate for the S.W. reef-crest.

It is probable that many factors contribute to the variation in fission rate with habitat, and these may include temperature, exposure, current flow, food availability, or more complex factors such as "patchiness" of resource distribution within a habitat, or possible genetic differences between populations. The latter would depend on a limited flow of genetic material between populations, and may not be compatible with the existence of free-living planktotrophic larvae of *H. atra*.

Ebert (1978) suggested that asexual reproduction accounts for the absence of large *H. atra* on the reef flat at Enewetak Atoll, and that fission is promoted by environmental factors. He interpreted the high rate of asexual reproduction in *H. atra* as an adaptation to the low recruitment rate from the sexual phase. *H. atra* is common at both Enewetak Atoll and Heron Island, and the high frequency of asexual reproduction may contribute to its abundance.

Data on changes in frequency of asexual reproduction over time in some habitats, and data on changes in regeneration states over time, indicate that fission is more frequent during limited periods of the year. Whether this change in frequency follows a yearly cycle cannot be determined from the data available.

Bonham and Held (1963) suggested that sexual reproduction may be seasonal, while asexual reproduction by binary fission could occur throughout the year. This study shows that both sexual and asexual reproduction may occur at low frequencies throughout the year, but with highest frequency of each during one or more limited periods.

Size-frequency distributions can be correlated with frequency of asexual reproduction. In areas of high fission frequency, samples were generally bimodally distributed, and in areas of low fission frequency, a unimodal distribution was most common. The lower peak of the

bimodal distributions were composed of individuals weighing less than 90 g, and a large proportion of these were products of asexual reproduction. Absence of age classes in the size-frequency distributions could be related to the relative importance of recruitment of fission products to the population.

In some organisms, growth has been estimated by obtaining growth increment data from tagged individuals, and applying growth equations such as the Brody-Bertalanffy equation. This method has been successfully applied to echinoids (Ebert, 1977) using tetracycline tagged skeletal elements, and has been tested on holothurians (Ebert, 1978). These analyses of growth are complicated when individuals undergo asexual reproduction. Calcification rates, used as an estimator of growth, may not be uniform in former oral and former anal ends. The size of the calcareous plates will have no relationship with the overall size of the animals, so most growth equations become inapplicable. If individuals divide more than once in their lifetime, mortality may be impossible to define or measure.

Overall, the unusual growth and reproductive characteristics of this species indicate that traditional growth analyses have little value in obtaining meaningful data on growth and mortality.

ACKNOWLEDGEMENTS

I thank Dr Ann Cameron and Mr Russell Reichelt for their valuable advice and assistance during the course of this study, and for critically reading the manuscript. I acknowledge Mr Richard Martin and Dr Peter Dwyer for their helpful suggestions, and thank my friends for assistance in the field. The use of facilities at the Heron Island Research Station is gratefully acknowledged.

REFERENCES

- Bacci, G., 1965. Sex Determination. Pergamon Press, Oxford.
- Bakus, G. J., 1973. The biology and ecology of tropical holothurians. In Jones and Endean (eds.), *Biology and Geology of Coral Reefs*, Vol. 2: 325-367. Academic Press, New York.
- Bonham, K. and E. E. Held, 1963. Ecological observations on the sea cucumbers *Holothuria atra* and *H. leucospilota* at Rongelap Atoll, Marshall Islands. *Pacif. Sci.*, 17: 305-314.
- Booolootian, R. A. 1966. Reproductive physiology. In R. A. Booolootian (ed.), *Physiology of Echinodermata*: 561-614. Interscience Publishers, New York.
- Crozier, W. J., 1917. Multiplication by fission in holothurians. *Am. Nat.*, 51: 560-566.
- Deichmann, E., 1922. On some cases of multiplication by fission and of coalescence in holothurians. *Vidensk. Meddr. dansk naturh. Foren.*, 73: 199-204.
- Ebert, T. A., 1977. An experimental analysis of sea urchin dynamics and community interactions on a rock jetty. *J. exp. mar. Biol. Ecol.*, 27: 1-22.
- 1978. Growth and size of the tropical sea-cucumber *Holothuria (Halodeima) atra* Jaeger at Enewetak Atoll, Marshall Islands. *Pacif. Sci.*, 32(2): 183-191.
- Green, J. D., 1978. The annual reproductive cycle of an apodous holothurian, *Leptosynapta tenuis*: a bimodal breeding season. *Biol. Bull.*, 154: 68-78.
- Hyman, L. H., 1955. The Invertebrates: Echinodermata. The Coelomate Bilateria. Vol. 4: 1-763. McGraw-Hill, New York.
- Krishnaswamy, S. and S. Krishnan, 1967. A report on the reproductive cycle of the holothurian *Holothuria scabra* Jaeger. *Curr. Sci.*, 36: 155-156.

- Pearse, J. S., 1968. Patterns of reproductive periodicities in four species of Indo-Pacific echinoderms. *Proc. Indian Acad. Sci., Sec. B.*, 67: 247-279.
- 1974. Reproductive patterns of tropical reef animals: three species of sea urchins. *Proc. 2nd Int. Coral Reef Symp.* 1: 235-240.
- Stephenson, A., 1934. The breeding of reef animals. Part II. Invertebrates other than corals. *Scient. Rep. Gt. Barrier Reef Exped.*, (1928-29), 3(9): 117-128.
- Tanaka, Y., 1958. Seasonal changes occurring in the gonad of *Stichopus japonicus*. *Bull. Fac. Fish Hokkaido Univ.*, 9: 29-36.

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